# Enhancing the benefits to biodiversity and ecosystem services within arable field margins

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December 2017

A thesis submitted for the degree of Doctor of Philosophy

# Declaration

I herewith declare that this thesis has been written by myself and that it embodies the results of my own research. No content herein has previously been submitted to obtain a degree in any form. Where appropriate, the nature and extent of work carried out in collaboration with others is acknowledged.

Mark A. Ashby,

Lancaster, United Kingdom, December 2017.

# Acknowledgements

This thesis was co-funded by Waitrose Ltd UK and the Biotechnology and Biological Sciences Research Council (BBSRC), as part of a four-year Doctoral Training Partnership PhD project. The successful completion of this PhD is the result of a tremendous amount of assistance, input and encouragement from, what seems like, a battalion of helpful people. As such, I would like to express my sincere gratitude to all of those who have been involved. First and foremost, I would like to thank all three of my PhD supervisors for their support and guidance. Carly for consistently offering her time, knowledge and patience to review endless chapter drafts and to really push me towards the finish line. Andy, for helping me to draw out the key messages from a large dataset and ironing out statistical problems. And Simon, who despite his ludicrously busy schedule, has always made time to provide thoughtful and inciteful comments on fieldwork protocols, findings and thesis content, usually from some far-off exotic location.

I would like to thank Alan Wilson, technical manager in agronomy for Waitrose Ltd, for his continual interest in the project and for inviting me to speak every year at the Waitrose Science Conference. I am indebted to Professor Chris Stoate from the Game and Wildlife Conservation Trust (GWCT) and Brin Hughes from Conservation Grade, who were both instrumental in helping me to find the study farms I required to conduct this project. This brings me to the farmers who, not only gave me permission to use their farms as study sites, but also put up with my constant questions about crop rotations and margin management for four solid years, and even held back from cutting my plots until I finished data collection. For this, I thank you all. However, several farmers deserve a special mention. Mr Mumford at Agden Green Farm towed my car out of a very deep ditch during the 2014 field season, then almost a week later Mr Parker at Highfield Farm kindly offered me the same favour. Car trouble was also kindly fixed by Mr King at Hay Farm in April 2017 (this time it was a flat battery).

My thanks also go to Professor John Holland (also from GWCT), who was extremely helpful in answering many of my methodological questions regarding the use of sentinel prey. Furthermore, I would like to thank three fieldwork and lab assistants who have helped with various aspects of this PhD: Charlotte Warburton, Kathryn Hinton and Kate Morgan. In truth, I am particularly indebted to Kate, because without her constant monitoring and harvesting of my strawberry phytometers when they were brought back from the field, I would not have been able to collect as much data as I did in 2016. Finally, I would like to express my sincerest thanks and gratitude to my partner Stacey. She has been an invaluable field assistant and a

beacon of positivity, support and understanding when this project seemed to consume my life. The successful completion of this project owes more to her than she realises.

# Abstract

We need to move towards more sustainable farming methods that maximise yields whilst protecting the environment. One approach that would achieve this goal is ecological intensification, which seeks to manage the biodiversity and ecological processes underpinning agricultural production so that damaging farming practices can be replaced or reduced. Forb-rich arable field margins have been shown to benefit flower-visiting insects such as wild bees, and recent evidence suggests that they can also enhance the levels of pollination and pest control in adjacent crop fields. They may also promote a suite of additional ecosystem services of societal and agronomic importance, but this has yet to be established. Furthermore, the ability of forb-rich field margins to deliver multiple benefits (*i.e.* ecosystem multifunctionality), including pest control and pollination, is likely to be contingent on a range of local and landscape factors. Using a range of pre-existing field margin plots ($n$ = 98) distributed across 16 arable farms in central eastern England, this study first sought to examine whether high quality forb-rich field margins promote ecosystem multifunctionality more effectively than low quality forb-poor field margins. This involved measuring a range ecosystem services within and adjacent to field margin plots, including pest control, pollination, soil carbon storage, flood alleviation, the abundance of invertebrate ecosystem service providers and the amount of invertebrate biodiversity. Secondly, it established whether arable field margins provide adequate foraging resources for flower-visiting insects. And thirdly, it determined the local and landscape factors (including margin quality) that best promote ecosystem service provision and invertebrate biodiversity within agro-ecosystems.

The findings indicated that quality was the most important determinant of ecosystem multifunctionality within arable field margins, as high quality margins supported significantly greater levels of pest control, pollination, flood alleviation and invertebrate biodiversity. However, a range of additional local and landscape management prescriptions further enhanced the multifunctionality of arable field margins, such as the level of vehicle traffic margins receive, vegetation height, landscape complexity and the amount of floral resources provided by the adjacent hedgerow. Despite the multiple benefits of high quality field margins, they were also found to enhance invertebrate crop pests. This may reduce the willingness of farmers to adopt forb-rich habitats on their land. Finally, the present study highlights that more consideration should be given to the forb species included within field margin seed mixes, as certain species were found to promote agronomically damaging crop pests, whereas other species not currently included in field margin seed mixes were extremely

attractive to several important flower-visiting taxa or flowered during spring; a period in which field margins are floristically poor.

This thesis clearly demonstrates that forb-rich field margins provide multiple agronomic, societal and biodiversity benefits, and outlines the important drivers of ecosystem multifunctionality. As such, it provides farmers and landowners with a clear set of management guidelines for promoting biodiversity and ecosystem services within arable field margins.

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# Chapter 1: General introduction

### 1.1 We must change the way we farm

During the second half of the twentieth century, agricultural intensification has been extremely successful in meeting the rising demand for cheap and affordable food (Godfray et al., 2010, Foley et al., 2011). But the expanding cropping units and increased external inputs associated with intensive agriculture mean that it is now one of the main drivers of biodiversity loss, ecosystem degradation and global environmental change (Foley et al., 2011, Tilman et al., 2011, Phalan et al., 2016). This has created a negative feedback loop whereby these processes threaten the very food production systems that help to generate them (Diaz et al., 2006, Power, 2010, Tai et al., 2014). Population growth and changes in diet preferences over the next fifty years will further exacerbate the global demand for food (Tilman et al., 2011, Tilman and Clark, 2015). However, if the current paradigm of agricultural intensification is pursued to meet these demands, then the negative feedback loop is likely to intensify and we may fail in our ability to feed a growing population (Godfray et al., 2010). To avoid this scenario, we need to change the way food is produced (Tilman et al., 2011). Harnessing the components of biodiversity that are essential for agricultural production could be part of the solution (Bommarco et al., 2013, Harrison et al., 2014, Garibaldi et al., 2017).

### 1.2 Ecological intensification as a new way forward

Utilising biodiversity to increase crop yields has been labelled 'ecological intensification' (Bommarco et al., 2013). This farming system aims to manage the biodiversity and ecological processes that underpin agricultural production so that damaging agrochemical inputs and methods can be replaced and/or supplemented (Potts et al., 2015). Unlike other environmentally friendly farming systems, ecological intensification aims to maximise beneficial ecological processes, habitat heterogeneity and non-farmed species diversity at multiple spatial and temporal scales (Garibaldi et al., 2017) (Table 1.1). Over recent decades, ecological intensification has been increasingly cited as a way of maximising yields whilst mitigating environmental damage (Cassman, 1999, Dore et al., 2011, Bommarco et al., 2013). This makes ecological sense, because we now know that farmland biodiversity is integral to agricultural production in a myriad of ways through its provision of important 'ecosystem services' (Zhang et al., 2007, Power, 2010).

**Table 1.1.** The contrasting methods of four major farming systems posited as solutions to tackle rising demands for food. Reproduced from Garibaldi et al. (2017).

| | Ecological intensification | Conventional intensification | Sustainable intensification | Organic farming |
|---|---|---|---|---|
| Use of synthetic inputs | - + | + + + | + + + | - + |
| Use of GMOs | - + | + + | + | - - - |
| Use of livestock | + | - + + | - + | - + |
| Utilises livestock and crop diversity | + + + | - + | - + | + |
| Promotes non-farmed biodiversity | + + + | - + + | + | + |
| Enhances habitat heterogeneity | + + + | - + | + | + |
| Utilises beneficial ecological processes | + + + | - + | + | + + |
| Builds in ecosystem resilience | + + + | - + | + | + |
| Enhances ecological processes at multiple temporal and spatial scales | + + + | - + | - + | - + |

- - -, never; - +, rarely; - + +, sometimes rarely; +, sometimes; + +, sometimes often; + + +, often

The Millennium Ecosystem Assessment (2005) defines ecosystem services as the benefits people derive from ecosystems and classifies them into four discrete categories: (i) provisioning services, *e.g.,* food, fibre, fuel and clean water; (ii) regulating services, *e.g.,* pollination, pest control, soil protection, pollution amelioration and water purification; (iii) cultural services, *e.g.,* spiritual values, education, and recreation; and, (iv) supporting services, *e.g.,* photosynthesis, nutrient cycling, soil formation and water cycling. Agro-ecosystems are primarily managed to optimise provisioning ecosystem services, such as food, fibre, and fuel, which are themselves dependent upon a wide variety of supporting and regulating services mediated by farmland biodiversity (Figure 1.1) (Zhang et al., 2007, Power, 2010). Moreover, in addition to augmenting agricultural production, farmland biodiversity also delivers a range of provisioning, regulating and cultural ecosystem services that are of benefit to wider society (Power, 2010, Firbank et al., 2013) (Figure 1.1).

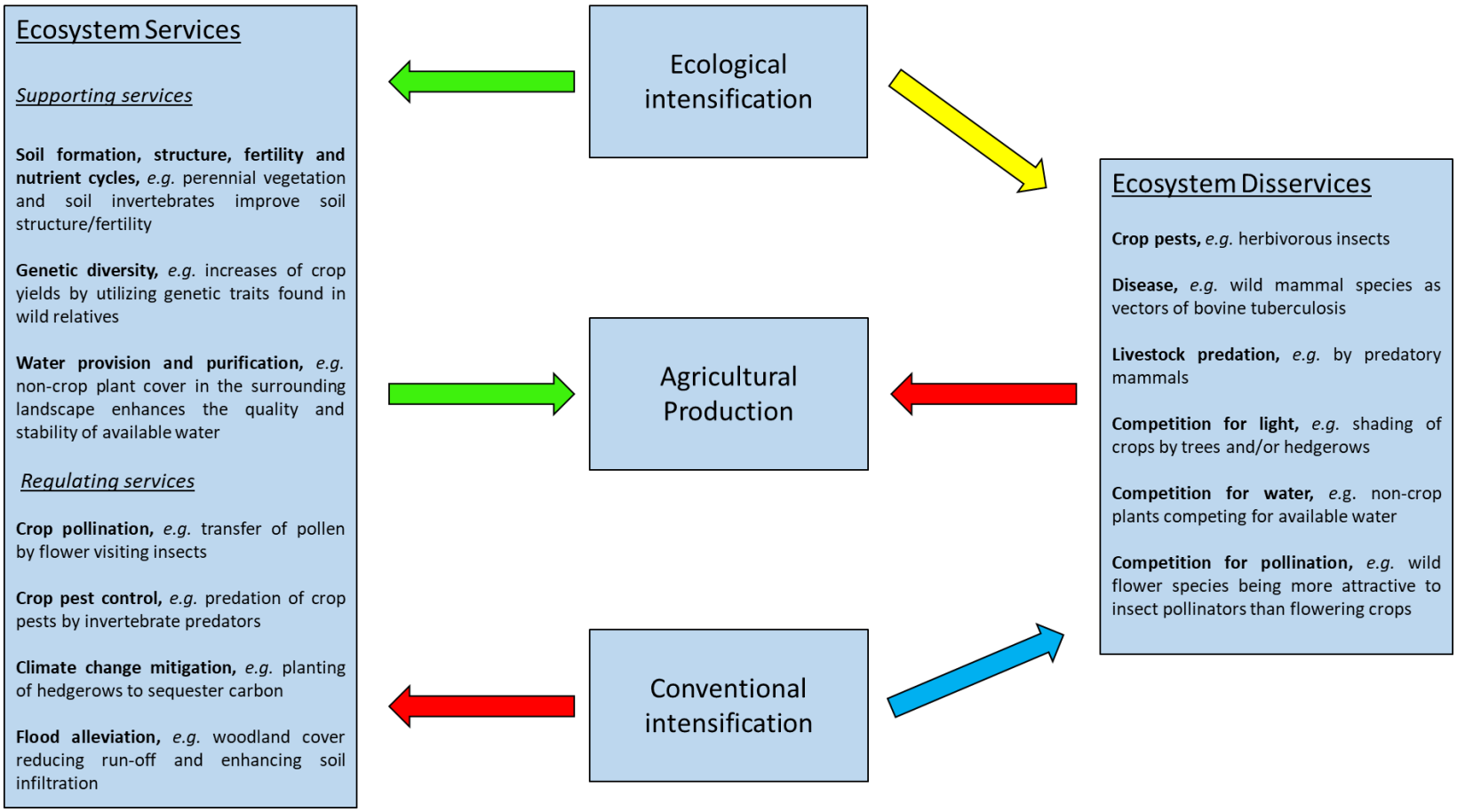


**Figure 1.1.** Relationships between ecological intensification, conventional intensification, farmland biodiversity, ecosystem service/disservice provision and agricultural production. Green arrows indicate a net positive effect, red arrows indicate a net negative effect, yellow arrows indicate an unknown but likely net negative effect and blue arrows indicate an unknown but likely net positive effect (Zhang et al., 2007, Power, 2010, Bommarco et al., 2013).

### 1.3 Farmland biodiversity and ecosystem service provision

*1.3.1 Provisioning services*

In northern Europe, the main provisioning service provided by farmland biodiversity is in the form of wild (*e.g.* deer, rabbits, hare and waterfowl) and managed (*e.g.* pheasants, grouse and partridges) game. Traditionally, rural populations utilised the uncropped vegetative elements of farmland biodiversity (*e.g.* hedgerows, hedge verges and woodland) to harvest fuel (*e.g.* wood), food for themselves (*e.g.* fruits, berries, nuts, herbs) and their livestock (*e.g.* leaf hay), and materials to aid in animal husbandry (*e.g.* fenceposts, timber and animal bedding) (Baudry et al., 2000, Marshall and Moonen, 2002, Holl et al., 2012, Firbank et al., 2013). Whilst some of these activities still exist on a small-scale (*e.g.* the harvesting of hedgerow fruits, berries and nuts), the overall use of these products has declined in northern Europe (Baudry et al., 2000). The importance of farmland biodiversity in delivering provisioning ecosystem services to wider society is likely to be greater within the small-scale agro-ecosystems characteristic of developing nations (Millennium Ecosystem Assessment, 2005).

*1.3.2 Supporting ecosystem services*

Soil formation, retention, structure and fertility are amongst the most crucial ecosystem services supporting agricultural production (Zhang et al., 2007, Adhikari and Hartemink, 2016). These services are largely driven by the activities of microorganisms and invertebrates present within cultivated soils (Barrios, 2007, Bardgett et al., 2014), but plants also play a key role in these processes (Fageria et al., 2005, Bardgett et al., 2014, Blanco-Canqui et al., 2015). For example, earthworms and other soil invertebrates improve soil structure via their burrowing activity, and their feeding activity incorporates organic matter into the soil which contributes to soil formation and increases soil fertility (Barrios, 2007, Blouin et al., 2013, Schon et al., 2017). Soil bacteria increase plant-available nitrogen via atmospheric nitrogen fixation, which, in most cases, is mediated by a symbiotic relationship with plants, especially those within the Fabaceae (legumes) family (Vitousek et al., 2002). As such, leguminous cover crops are often used to improve soil fertility (Fageria et al., 2005). Whilst soil formation, structure and fertility are important for crop growth, retention of soil is fundamental for keeping nutrients *in situ* and available to crops (Barrios, 2007, Zhang et al., 2007). Cover crops can also be used to retain soil and nutrients across crop rotations (Blanco-Canqui et al., 2015), and field boundary elements such as hedgerows and grass buffer strips minimise soil erosion from fields (Marshall and Moonen, 2002, Yuan et al., 2009).

Agriculture relies on the provision of clean water (Zhang et al., 2007, Power, 2010). Indeed, food production accounts for 70% of freshwater use globally (Foley et al., 2011). Biodiversity, in the form of increased tree cover across upstream watersheds, can increase the quality and seasonal stability of water available to farmland situated downstream (Guo et al., 2000, Maes et al., 2009). Furthermore, the creation of on-farm wetlands, and their associated plant communities, help to conserve and purify water for use within crop irrigation systems (Kay et al., 2009). Approximately 80% of water used within agro-ecosystems is derived from rainfall captured and stored in the soil (Molden, 2007), with soil water-storage capacity being enhanced by increases in soil organic matter content mediated by vegetative cover (*e.g.* via seasonal litter input) and the activity of soil biota (*e.g.* via incorporation of surface litter during burrowing and feeding) (Gregorich et al., 1994, Barrios, 2007, Power, 2010).

### *1.3.3 Regulating ecosystem services flowing from biodiversity to agriculture*

Pollination and pest control are perhaps the two best known ecosystem services flowing from farmland biodiversity to agriculture (Bianchi et al., 2006, Klein et al., 2007, Gallai et al., 2009, Holland et al., 2012, Rader et al., 2016). Strikingly, the yield and quality of 75% of crop species globally is dependant to a greater or lesser extent on the pollinating insects that visit crop flowers for food (Klein et al., 2007, Garratt et al., 2014a, Klatt et al., 2014, Rader et al., 2016). Moreover, a complete loss of pollinators would lead a 3-8% decrease in global agricultural production (Aizen et al., 2009). For some pollinator-dependant crops, yield is enhanced by the presence of a more functionally and taxonomically diverse flower-visiting community (Klein et al., 2003, Hoehn et al., 2008). In northern Europe, wild bee species and managed honeybees (*Apis mellifera*) are the most valuable pollinators within agro-ecosystems (e.g. Klatt, 2013, Garratt et al., 2014a, Garratt et al., 2014b, Klatt et al., 2014, Rader et al., 2016), but, depending on the crop, hoverflies (Syrphidae) and other Diptera may also be agronomically important (Jauker et al., 2012, Orford et al., 2015).

Invertebrate natural enemies can increase crop yields and reduce insecticide inputs by suppressing economically damaging crop pests (Ostman et al., 2003, Birkhofer et al., 2016). A wide range of invertebrate taxa are known natural enemies, including predatory beetles (*e.g.* Carabidae, Staphylinidae and Coccinellidae), spiders (Araneae), hoverfly larvae, predatory non-Syrphid Diptera (*e.g.* Empididae, Scathophagidae and Dolichopodidae), lacewings (Chrysopidae), predatory mites (Acari), parasitoid wasps (*e.g.* Ichneumonidae), predatory wasps (*e.g.* Vespidae), ants (Formicidae), predatory bugs (Heteroptera), centipedes

(Chilopoda) and harvestmen (Opiliones) (Bianchi et al., 2006, Holland et al., 2008, AHDB, 2014). Whilst many of these taxa may contribute to natural pest control, in cereal crops, aerial and canopy-active natural enemies, such as predatory Diptera, are more effective at controlling pest outbreaks (Holland et al., 2008, Holland et al., 2012). By enhancing yield and reducing synthetic inputs, the pollination and pest control services mediated by farmland invertebrates have been estimated to be worth around US$215 billion and US$4.5 billion per year, respectively (Losey and Vaughan, 2006, Gallai et al., 2009).

Modern agriculture is a significant contributor to anthropogenic climate change (Foley et al., 2005, Foley et al., 2011, Smith, 2012), localised flooding (O'Connell et al., 2007, Marshall et al., 2014) and the degradation of freshwater and marine ecosystems (Millennium Ecosystem Assessment, 2005, Moss, 2008, Carpenter et al., 2011, Chislock et al., 2013). These processes represent a direct threat to food production as well as wider society (Rockstrom et al., 2009, Alderman et al., 2012), but they can be mitigated by the appropriate management of farmland biodiversity (Falloon et al., 2004, Zhang et al., 2007, Smith et al., 2008b, Kay et al., 2009, Stoate et al., 2009, D'Acunto et al., 2014). For example, the planting of herbaceous or woody buffer strips at the field edge or adjacent to watercourses will trap and retain harmful agrochemical compounds and prevent them from entering aquatic ecosystems (Kay et al., 2009, Stoate et al., 2009). Woody and herbaceous buffer strips, as well as the soil organisms they support, may also reduce run-off via improvements to soil structure (*e.g.* increased porosity) and water retention (*e.g.* increased organic matter) (Barrios, 2007, Power, 2010, Fischer et al., 2014, Marshall et al., 2014, Fischer et al., 2015). In doing so, they potentially help to alleviate localised and downstream flooding (Marshall et al., 2014). Furthermore, areas of permanent vegetative cover (*e.g.* hedgerows and field margins) have the potential to sequester atmospheric carbon and nitrogen because they facilitate the accumulation of soil organic matter by having lower soil disturbance regimes (*i.e.* they are not ploughed) and above-ground biomass is left *in situ* (*i.e.* vegetation is not harvested) (e.g. Falloon et al., 2004, De Deyn et al., 2011, D'Acunto et al., 2014). These areas also produce lower $N_2O$ emissions compared to cultivated land because they receive lower fertiliser inputs and have higher rates of $CH_4$ oxidation (Smith et al., 2008b).

### *1.3.4. Cultural services*

One often overlooked element of farmland biodiversity is its cultural value to society. Cultural ecosystem services include recreational value, aesthetic enjoyment, historical importance,

spiritual fulfilment and education (Millennium Ecosystem Assessment, 2005). In general, biodiversity can be considered a cultural ecosystem service, since the appreciation of nature is recognised by most societies as an inherent human value (Zhang et al., 2007). Viewing or experiencing biodiversity can also deliver substantial health benefits, such as increased psychological well-being (Fuller et al., 2007), social interaction (Sullivan et al., 2004) and patient recovery (Ulrich, 1984). Since agriculture represents the dominant land use in the UK, it is often adjacent to human habitation. And so, people are more likely to experience biodiversity on farmland than in any other habitat (Bradbury et al., 2010). This suggests that the majority of UK's cultural ecosystem services are currently provided by farmland wildlife.

Specific examples of the cultural services provided by farmland biodiversity in the UK include wild and managed farmland bird populations, which provide recreation value in the form of gamebird hunting and bird watching, and butterflies and moths, which provide aesthetic enjoyment and spiritual fulfilment (Bradbury et al., 2010, UK National Ecosystem Assessment, 2011, King et al., 2017). Landscape features created by the vegetative component of farmland biodiversity, such as hedgerows, green lanes and woodlands, provide immense aesthetic, spiritual and historical value (Burel and Baudry, 1995, Belsey, 1998, Stoate et al., 2001, Stoate et al., 2009, UK National Ecosystem Assessment, 2011). For example, in England many people regard hedgerows as a quintessential feature of the countryside (Oreszczyn and Lane, 2000). As such, they are viewed as part of the English national identity and contribute to a strong sense of place (*ibid*). They also possess historical value, since many date back to the Saxon era in Britain and often delimit parish boundaries (Pollard et al., 1974, Firbank et al., 2013).

### *1.3.5 Ecosystem disservices flowing from biodiversity to agriculture*

Whilst it is vital to emphasise the beneficial role of farmland biodiversity, we should not overlook the fact that in some instances it can increase production costs and reduce yields (Frank, 1998, Eggenschwiler et al., 2013, Rusch et al., 2013b). Salient examples of these 'ecosystem disservices' include the damage to crops caused by insect pests and competition for resources by weeds (Figure 1.1) (Oerke, 2006, Oliveira et al., 2014). Interestingly however, the methods employed under intensive agriculture can simultaneously degrade important ecosystem services whilst exacerbating disservices (Matson et al., 1997, Zhang et al., 2007, Power, 2010). Two such examples include how the over reliance on insecticides and the removal of uncropped land contribute to pest outbreaks via increased genetic resistance and

the reduction of natural enemies (Bianchi et al., 2006, Dyer, 2014). In contrast, by promoting specific components of farmland biodiversity, ecological intensification may remove the impact of certain ecosystem disservices (Bommarco et al., 2013). A case in point is when yield losses to insect pests are reduced by the creation of natural enemy habitat and the concomitant increases in natural enemy populations (Tschumi et al., 2016a). But to date, our understanding of the relationships between conventional intensification, ecological intensification and ecosystem dis/services remain incomplete (Figure 1.1).

**1.4 Threats to farmland biodiversity and ecosystem service provision**

By facilitating a range of ecosystem services, farmland biodiversity clearly plays a key role in agricultural production, environmental protection and human well-being (Zhang et al., 2007, Power, 2010, Bommarco et al., 2013, Firbank et al., 2013). But despite its importance, biodiversity within agricultural areas in the UK is under threat: farmland birds have declined by 54% since 1970, many invertebrates including bees, butterflies and moths are in decline, and plant diversity has decreased within arable land, permanent pasture and field boundaries (Robinson and Sutherland, 2002, Biesmeijer et al., 2006, Carey et al., 2008, Carvalheiro et al., 2013, Hayhow et al., 2016). Whilst these declines can be attributed to multiple causes associated with the intensification of agricultural practices, habitat loss is probably the most pervasive threat (e.g. Stoate et al., 2001, Robinson and Sutherland, 2002, Tscharntke et al., 2005, Donald et al., 2006, Firbank et al., 2008, Stoate et al., 2009). The systematic removal or conversion of uncropped land to agriculture since the end of the Second World War has resulted in the loss and fragmentation of wildlife habitats (Robinson and Sutherland, 2002, Tscharntke et al., 2002, Benton et al., 2003, Haines-Young et al., 2003). These processes are consistently found to have a negative effect on farmland biodiversity (Benton et al., 2003, Diekotter et al., 2008, Fahrig et al., 2015, Gamez-Virues et al., 2015). This is because uncropped land provides wildlife with the resources it needs to survive, whereas intensive agricultural fields are largely resource-poor environments (Landis et al., 2000, Bianchi et al., 2006, Vickery et al., 2009, Roulston and Goodell, 2011). For beneficial invertebrates such as insect pollinators and natural enemies, uncropped areas provide overwintering/nest sites, larval habitat, alternative insect prey, and pollen and nectar (Landis et al., 2000, Bianchi et al., 2006, Lye et al., 2009, Cole et al., 2017). Consequently, simplified agro-ecosystems containing a low proportion of uncropped land support smaller numbers of insect pollinators and natural enemies and also receive lower levels of crop pollination and natural pest control (Ricketts,

2001, Ricketts, 2004, Chaplin-Kramer et al., 2011, Shackelford et al., 2013, Rusch et al., 2016b). It is also worth noting that, given the beneficial effect areas of perennial vegetation have on a range of important ecological processes (e.g. soil carbon storage and flood alleviation, D'Acunto et al., 2014, Marshall et al., 2014), the historic losses of uncropped land may have greatly reduced the capacity of modern agro-ecosystems to deliver multiple ecosystem services (Swinton et al., 2007, Firbank et al., 2013).

**1.5 Habitat creation to enhance farmland biodiversity and ecosystem services**

At present, the principle method for enhancing and maintaining farmland biodiversity in Europe is through the implementation of agri-environment schemes (AES), which offer farmers and landowners a financial reward to create and/or sympathetically manage areas of uncropped land (Whittingham, 2007, Whittingham, 2011). A large area of research is devoted to the potential wildlife benefits of AES, and how individual schemes can be optimised for maximum biodiversity gain (Carvell et al., 2007, Woodcock et al., 2007a, Smith et al., 2008a, Batary et al., 2015, Westbury et al., 2017). Nevertheless, the extent to which AES options enhance farmland biodiversity is disputed (Kleijn et al., 2006, Kleijn et al., 2011, Whittingham, 2011). This is for several reasons. Firstly, their effectiveness is dependent upon the surrounding landscape, with schemes having the greatest effect on biodiversity when implemented in simple (1–20% semi-natural habitat), rather than cleared (<1% semi-natural habitat) or complex agro-ecosystems (>20% semi-natural habitat) (Tscharntke et al., 2005, Kleijn et al., 2011, Scheper et al., 2013, Scheper et al., 2015). Secondly, the AES options with the highest uptake in the UK are those which are easy to implement (*i.e.* they require little time/effort/resources), such as sympathetic hedgerow management or the creation of grass buffer strips (DEFRA, 2013, Natural England, 2013a). But these schemes deliver little biodiversity benefit compared to more labour-intensive AES that provide targeted taxa-specific habitat resources (Carvell et al., 2004, Carvell et al., 2015, Pywell et al., 2015, Wood et al., 2015c).

A salient example of a targeted AES option is the creation of forb-rich arable field margins, which are designed to provide foraging resources for flower-visiting insects (Haaland et al., 2011). Results from a wide-range of studies indicate that, compared to general, untargeted AES, and/or crop fields, forb-rich arable field margins increase the local abundance, density and richness of several flower-visitors, including important crop pollinators and natural enemies (e.g. Haaland et al., 2011, Grass et al., 2016, Tschumi et al.,

2016b). Moreover, an increasing body of research highlights the positive effect forb-rich field margins can have on pollination and pest control in the adjacent crop (Blaauw and Isaacs, 2014a, 2015, Woodcock et al., 2016a, Sutter et al., 2017a). At present, uptake of forb-rich AES options remains low in England: they comprise less than 5% of arable land (DEFRA, 2013). However, it is likely that uptake will increase if the agronomic benefits of forb-rich margins are more consistently demonstrated (Wratten et al., 2012, Bommarco et al., 2013).

Typically, studies examining the effect of forb-rich field margins on insect flower-visitors usually focus on a narrow range of beneficial and prominent taxa, including bumblebees (*Bombus* spp.) (Carvell et al., 2004, Carvell et al., 2006, Carvell et al., 2007), and less frequently, hoverflies (Syrphidae) (Haenke et al., 2009) and solitary bees (Scheper et al., 2015). In fact, many of the forb species included in AES seed mixes are the preferred forage plants of bumblebees (Kells et al., 2001, Carvell et al., 2004, Pywell et al., 2005b, Carvell et al., 2006, Pywell et al., 2006, Carvell et al., 2007, Pywell et al., 2011). This suggests that AES flower margins may not be benefitting the wider flower-visiting community as much as they could be (see, for example Jervis et al., 1993, Wood et al., 2016). But we lack data on both the full range of flower-visiting taxa that forb-rich margins currently support and whether current AES seed mixes provide sufficient pollen and nectar resources for taxa other than bumblebees. Furthermore, the almost exclusive focus on beneficial insects, also means we lack data about the extent to which forb-rich field margins support agronomically important crop pests (but see Eggenschwiler et al., 2013, Grass et al., 2016).

**1.6 Creating multifunctional field margins**

There has been a recent focus by ecologists on how the loss of biodiversity might impair ecosystem multifunctionality, *i.e.* the ability of an ecosystem/biotope to provide multiple ecological benefits simultaneously (e.g. Wagg et al., 2014, Lefcheck et al., 2015, Hautier et al., 2017). This focus stems from the fact that, in general, greater levels of biodiversity lead to higher levels of ecosystem functioning (e.g. Cardinale et al., 2012, Tilman et al., 2014, Hautier et al., 2015). Because the creation of forb-rich field margins increases local plant species richness, they therefore have the potential to promote ecosystem multifunctionality within agro-ecosystems. Indeed, by increasing local plant species richness, forb-rich margins will not only benefit flower-visiting insects and their associated ecosystem services (*e.g.* pest control and pollination), but they may also enhance flood alleviation (via increased infiltration capacity) and climate change mitigation (via increased carbon storage) (De Deyn et al., 2011,

Cong et al., 2014, Fischer et al., 2014, Fischer et al., 2015), as well as populations of damaging crop pests (Eggenschwiler et al., 2013, Grass et al., 2016, Moreira et al., 2016). Yet, no study to date has explored the full range of ecosystem services and disservices that forb-rich margins provide.

Forb-rich field margins clearly have the potential to increase crop yields whilst protecting the environment and delivering additional benefits to society. Their adoption by farmers would therefore be a significant step towards promoting ecological intensification within agro-ecosystems (Cassman, 1999, Bommarco et al., 2013, Garibaldi et al., 2017). Nevertheless, the ecosystem multifunctionality of arable field margins is also likely to be influenced other factors at both local and landscape scales (see, for example Woodcock et al., 2007b, Rundlöf et al., 2008a, Potts et al., 2009, Chaplin-Kramer et al., 2011, Sutter et al., 2017a). For example, the composition and complexity of the surrounding landscape can determine the levels of pollination and pest control delivered to crop fields (Chaplin-Kramer et al., 2011, Kennedy et al., 2013, Rusch et al., 2016b), and at local scales, factors such as cutting frequency and vegetation height can influence the abundance and richness of flower-visiting insects within field margin plots (Sjodin et al., 2008, Potts et al., 2009). Identifying the drivers that underpin the delivery of ecosystem services to crops and wider society would allow us to develop management guidelines for farmers wishing to promote ecological intensification and ecosystem multifunctionality (Bennett et al., 2009, Isaacs et al., 2009, Bennett et al., 2015).

### 1.7 Research aims and objectives

Farmland biodiversity can directly benefit agricultural production and wider society by mediating valuable ecosystem services. However, many important elements of farmland biodiversity are currently in sharp decline within the UK. This may threaten our ability to produce food and mitigate the harmful effects of global environmental change. The creation of forb-rich arable field margins has the potential to reverse these declines whilst also enhancing important ecosystem services including pollination, pest control, soil carbon storage and flood alleviation. However, no study to date has investigated this possibility. Moreover, we lack data on the local and landscape drivers of ecosystem multifunctionality within agro-ecosystems. Finally, previous research on AES forb-rich field margins has focussed on how they affect populations of beneficial and prominent flower-visitor taxa such as wild bees. Consequently, there is little data on whether they provide suitable foraging resources

for the wider flower-visiting community, nor do we know if they enhance agronomically damaging crop pests. The principle objective of this PhD is to provide farmers and land managers with a set of clear and specific recommendations that will maximise ecosystem service delivery (and minimise ecosystem disservices) within arable field margins. To achieve this objective, this project sought to:

1. Determine whether high quality forb-rich field margins deliver multiple ecosystem services more effectively than low quality forb-poor field margins (Chapter 3).

2. Investigate whether arable field margins currently provide sufficient foraging resources for flower-visiting insects (Chapter 3).

3. Examine how the proportion of different biotopes at the landscape scale influences invertebrate biodiversity and ecosystem service provision within arable field margins (Chapter 4).

4. Examine how landscape complexity and habitat connectivity influence invertebrate biodiversity and ecosystem service provision within arable field margins (Chapter 5).

5. Establish the key drivers (both local and landscape) promoting ecosystem service provision and invertebrate biodiversity within arable field margins (Chapter 6).

# Chapter 2: Site selection and methods

## 2.1 Study sites

Arable field margins have previously been defined as the outer six metres of the crop, any herbaceous margin strip present and the linear features associated with the boundary (*e.g.* hedgerow, shelterbelt, fence, ditch, stream or drain) (Marshall and Moonen, 2002). Here, they are defined as the herbaceous margin strip located at the field edge, between the crop and the field boundary. Project data collection took place between September 2014 and May 2017 on 16 predominantly arable farms with differing field sizes, landscape contexts and soil types. Study farms were widely distributed across six counties within two of the most important lowland arable regions within the UK (Figure 2.1): The East Midlands and Eastern England. Livestock grazing on permanent grassland took place on some of these farms, but arable and livestock areas were separated into discrete management blocks. Distances between study farms ranged between 3.39 and 113.92 km (mean distance ± SEM: 48.66 ± 2.38 km). Grid references for each study farm can be found in the Appendix (Table A1).

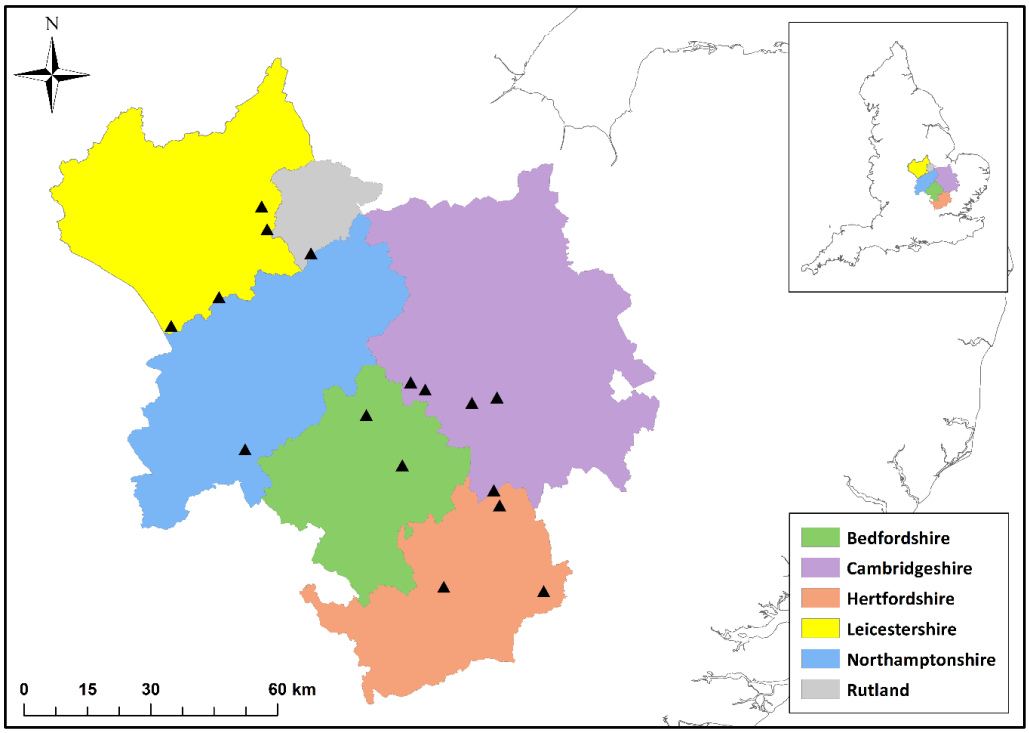


**Figure 2.1.** A map showing the location of the study area and the farms used (triangles) during this project.

During this project a total of 98 well established (>2 years old) field margin plots of varying widths were used, with either six (*n* = 14) or seven (*n* = 2) margin plots selected per farm. Within each farm, margin plots were situated either in different fields, opposite sides of a field or, in a few cases, discreet sides of the same field. Margin plots were 100 m in length and were positioned at least 25 m clear of field corners or hedgerow intersections, as these areas often have higher floral and faunal diversity owing to their more sheltered microclimatic conditions and lower disturbance (Dover, 1996, Dover et al., 1998, Maudsley, 2000). Margin plots were originally created by either natural regeneration, sowing of a grass only seed mixture or sowing of a seed mixture containing flowers. Due to crop rotations and logistics, data was collected from different combinations of margins/sites across years for different ecosystem service and biodiversity metrics (Table 2.1). Table A2 in the Appendix contains crop rotation information for each margin during different surveys and field experiments.

**Table 2.1.** A summary of the sites and margins used during different surveys and field experiments throughout this project.

| Sampling method | No of margins | Quality | No of Sites |
|---|---|---|---|
| Soil carbon, nitrogen and organic matter | 96 | 43 High, 53 Low | 16 |
| Infiltration measurements | 60 | 30 High, 30 Low | 16 |
| Pollination assay | 16 | 8 high, 8 low (paired) | 8 |
| Pest control assay | 16 | 8 high, 8 low (paired) | 8 |
| Pitfall trapping | 96 | 43 High, 53 Low | 16 |
| Transect surveys | 40 | 16 High, 24 Low | 13 |
| Sweep net surveys | 16 | 8 high, 8 low (paired) | 8 |

### 2.2 Selection and classification of field margin plots

To answer research question one, *"Do high quality field margins deliver ecosystem services more effectively than low quality field margins?"*, margin plots were selected according to their value as flower-visitor foraging habitat. A large body of empirical evidence suggests that early successional biotopes with an abundant and diverse flower community provide high quality foraging habitat for flower-visiting insects (Haaland et al., 2011, Scheper et al., 2013). Consequently, forb-rich margins were designated as 'high quality' and forb-poor margins were

designated as 'low quality'. Quality was defined in this way for three reasons. Firstly, it has been hypothesised that creating forb-rich biotopes on farmland to enhance flower-visiting insect populations will provide additional biodiversity and ecosystem service benefits (Blaauw and Isaacs, 2014a, Pywell et al., 2015, Balzan et al., 2016b). Despite such examples, few studies have examined whether forb-rich field margins can provide multiple ecological benefits simultaneously (*i.e.* multifunctionality) (but see Olson and Wackers, 2007, Sutter et al., 2017a). Secondly, most studies focus on the benefits of forb-rich field margins and often ignore the ecosystem dis-services they might support. For example, we know very little about the potential of forb-rich field margins to support populations of crop pests (but see Frank, 1998, Winkler et al., 2010, Balzan et al., 2016a, Balzan et al., 2016b, Grass et al., 2016). Thirdly, additional information on the biodiversity and ecosystem services provided by forb-rich field margins will help to highlight the ecological role they play, which may increase their uptake by farmers and will also facilitate a greater understanding of when and where their implementation will be most appropriate. (Wratten et al., 2012). For example, not only do forb-rich field margins support greater numbers of flower-visiting natural enemies than either margins that are forb-poor or crop edges (Haenke et al., 2009, Haaland et al., 2011, Campbell et al., 2017a), but they also increase pest suppression in the adjacent crop (Blaauw and Isaacs, 2015, Woodcock et al., 2016a). Furthermore, compared to forb-poor biotopes, forb-rich biotopes deliver better foraging resources for granivorous and insectivorous birds (Wood et al., 2013, Westbury et al., 2017), increased carbon and nitrogen storage (De Deyn et al., 2011), and greater levels of pollination (Orford et al., 2016).

Initially, margin plots were selected by conducting a rapid visual assessment of forb richness and cover. After selection, the percent cover of individual species was recorded within three 2 x 2 m quadrats placed at 25, 50 and 75 m along the centre of each 100 m plot (Figure 2.2). Only individuals rooted within the quadrat were recorded. In total, two vegetation surveys were carried out: one in August 2014 and one in July 2016. Percent cover values were averaged across the three quadrats during each survey, whereas plant richness and diversity values were calculated by summing the total number of species found within each margin plot during each survey year. Data from both surveys was averaged and then a quality Index was constructed for each field margin plot based on forb richness and forb cover (%). First, both variables were normalised using the following formula taken from Herzog et al. (2006):

$$((Yi - Ymin) \div (Ymax - Ymin)) \times 100$$

Where *Yi* is the observed value, *Ymin* is the minimum observed value and *Ymax* is the maximum observed value. After normalising forb richness and forb cover values for each margin, these variables were themselves averaged to give a quality index score. Using this index, a margin was classified as high quality if it had a score >30 (Figure 2.3). Quality index scores for individual margin plots used during this study are listed in Table A2 in the Appendix.

Low quality margins had index scores ranging from 0.96 to 25.11, whereas index scores for high quality margins ranged between 34.49 and 81.01. Mean index scores were also significantly greater within high quality margin plots ($\chi^2$ = 167.45, d.f. = 1, *P* <0.001; Table 2.2). In general, high quality margins were characterised by having: significantly greater vascular vegetation richness, forb richness, Shannon diversity and Simpson's diversity; significantly greater cover of forbs, Fabaceae and Asteraceae; and, significantly less cover of grasses (Table 2.2). In addition, quality was not always determined by the original seed mix used to create each field margin plot (Figure 2.4). For example, whilst 73.3% of margins designated as high quality were originally sown with a seed mixture containing forbs, 11.1% were originally sown with a grass only seed mixture and 15.6% were created by natural regeneration (Figure 2.4). In contrast, 50.9% of margins designated as low quality were originally left to naturally regenerate, 37.7% were originally sown with a grass only seed mixture and 11.3% were originally sown with a seed mixture containing forb species (Figure 2.4).

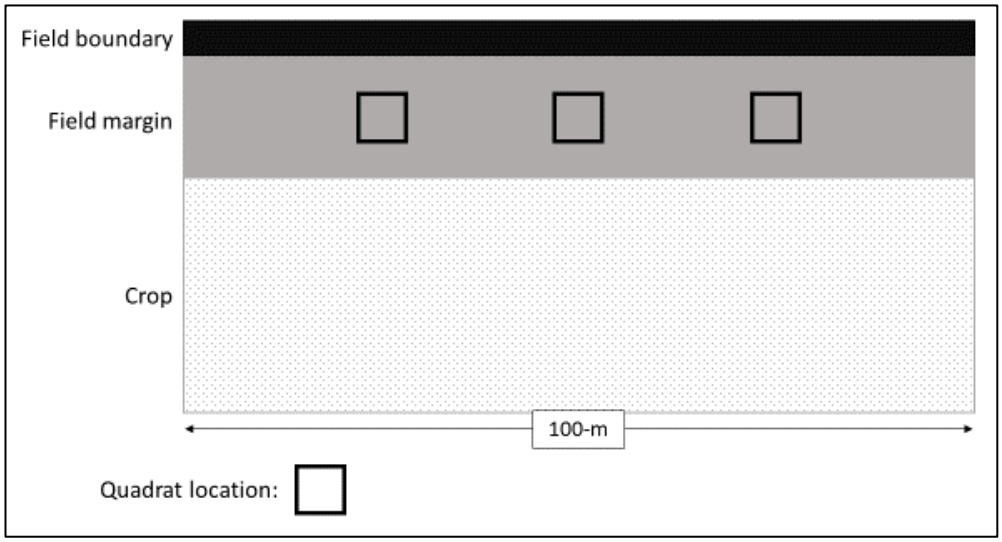


**Figure 2.2.** Schematic diagram showing vegetation quadrat locations within each field margin plot.

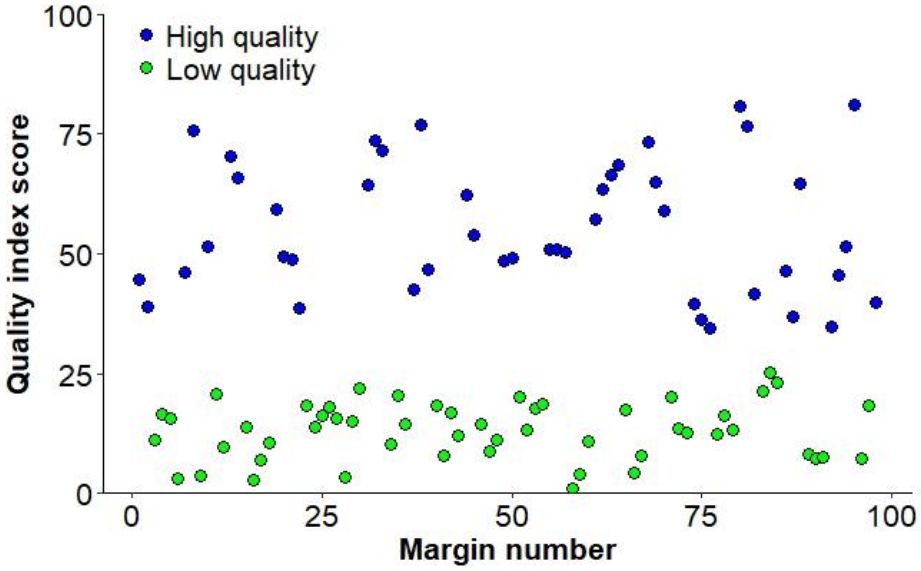


**Figure 2.3.** Quality index scores for individual high and low quality field margin plots used during this project.

**Table 2.2.** Mean (± SEM) difference in individual vegetation (a) richness, (b) diversity, (c) abundance and (d) margin quality metrics between high and low quality field margin plots. Chi-square test statistics and *P*-values are from linear/generalised linear mixed-effect model likelihood ratio tests with quality as a fixed effect and site as a random effect (d.f. = 1). Significant results (*P* <0.05) are presented in bold.

| Vegetation metric | High quality | Low quality | $\chi^2$ | *p* |
|---|---|---|---|---|
| *a) Richness metrics* | | | | |
| Vegetation species richness | 26.76 ± 1.14 | 16.53 ± 0.49 | **66.98** | **<0.001** |
| Forb species richness *[1] | 19.16 ± 0.76 | 8.91 ± 0.40 | **110.45** | **<0.001** |
| Grass species richness | 6.29 ± 0.41 | 6.42 ± 0.28 | 0.01 | 0.933 |
| *b) Diversity metrics* | | | | |
| Species evenness | 0.17 ± 0.00 | 0.16 ± 0.01 | 3.47 | 0.062 |
| Shannon-Weiner index | 1.99 ± 0.06 | 1.47 ± 0.05 | **39.95** | **<0.001** |
| Simpson's index | 0.70 ± 0.02 | 0.58 ± 0.02 | **14.70** | **<0.001** |
| *c) Abundance metrics* | | | | |
| Total forb cover (%) *[2] | 60.20 ± 3.86 | 8.29 ± 0.73 | **140.34** | **<0.001** |
| Fabaceae cover (%)[1] | 27.75 ± 4.31 | 1.02 ± 0.24 | **111.94** | **<0.001** |
| Apiaceae cover (%)[1] | 1.26 ± 0.32 | 1.31 ± 0.34 | 0.24 | 0.625 |
| Asteraceae cover (%)[1] | 17.02 ± 2.32 | 2.66 ± 0.38 | **59.56** | **<0.001** |
| Other forb cover (%)[1] | 14.17 ± 2.38 | 3.30 ± 0.52 | **42.84** | **<0.001** |
| Grass cover (%) | 39.35 ± 3.82 | 86.18 ± 1.72 | **98.41** | **<0.001** |
| *d) Margin quality index* | 55.42 ± 2.04 | 13.08 ± 0.81 | **167.45** | **<0.001** |

* Variables used to construct margin quality index scores

[1] Negative binomial (log-link) Generalised linear mixed-effect model

[2] ln(x) transformed for analysis

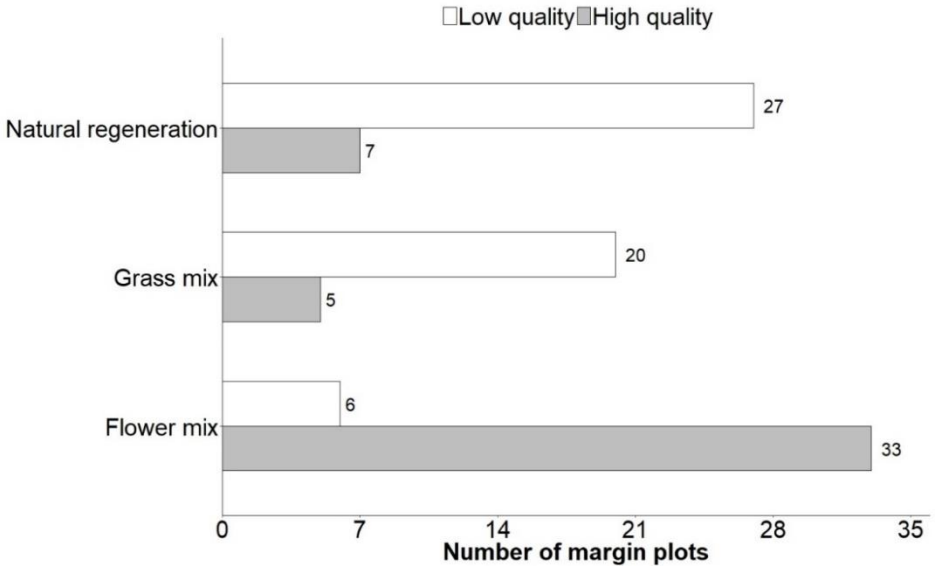


**Figure 2.4.** The number of high and low quality margin plots used during this study that were originally created by natural regeneration, sowing of a grass only seed mixture or the sowing of a seed mixture that included forb species.

### 2.3 Landscape mapping and analysis

To explore the effect of landscape context on ecosystem service provision and biodiversity, the quantity of different biotopes were mapped within 1 km, 500 m and 250 m radii around the centroid of each field margin plot. The total area mapped within each radii equalled 3.14, 0.79 and 0.20 $km^2$, respectively. Whilst the flight and foraging distances for some groups of flower-visiting insects studied during this project exceeds 1 km (Knight et al., 2005, Osborne et al., 2008a, Zurbuchen et al., 2010, Raymond et al., 2013, Mauchline et al., 2017), the average arable farm size in England is 2.07 $km^2$ (DEFRA, 2016a). Therefore, the maximum radii of 1 km (3.14 $km^2$) represents a more relevant management unit for famers than larger spatial scales, despite being ecologically redundant for some flower-visiting taxa.

Using a combination of field surveys, ordnance survey data and satellite imagery, detailed biotope maps were produced within Google Earth Pro (Google Inc.) at each spatial scale to a resolution of 2 $m^2$. Four broad biotope classifications were used: (1) arable land; (2) agricultural grassland; (3) urban land; and (4) uncropped land. These biotope classes are described in detail in Table 2.3 below. Google Earth biotope maps were exported to ArcGIS 10.4 (ESRI) and converted into raster maps with a spatial resolution of 0.5 x 0.5 m per cell (Figure 2.5). At each spatial scale, the percentage cover of each biotope class was calculated. Then Fragstats 3.3 (McGarigal et al., 2002) was used to calculate three additional landscape

complexity and habitat connectivity metrics: Shannon biotope diversity index (SHBI), mean patch shape index (shape index) and the connectance index between patches of uncropped land (uncropped connectance index). Detailed descriptions of these landscape metrics are outlined in Table 2.3.

**Table 2.3.** Description of the metrics used during landscape analysis.

| Landscape metric | Description |
|---|---|
| % Arable land | Percentage of landscape comprised of arable crops. |
| % Agricultural grassland | Percentage of landscape comprised of grassland that was grazed by livestock and/or cut for silage or hay. |
| % Urban land | Percentage of landscape comprised of roads, farm buildings, private houses and gardens. |
| % Uncropped land | Percentage of landscape comprised of rough grassland, scrub, woodland, field margins, hedgerows, ditches, ponds and rivers (*viz.* semi-natural habitat). |
| Shannon biotope diversity index (SHBDI) | A measure of landscape compositional complexity that equals minus the sum, across all biotope classes within a landscape, of the proportional abundance of each biotope class multiplied by that proportion (McGarigal et al., 2002). SHBDI equals zero when the landscape contains only one biotope class but increases as the number of different biotope classes increases (*i.e.* in complex landscapes) and/or the proportional distribution of area among biotope classes becomes more equitable (McGarigal et al., 2002). |
| Shape index | A measure of landscape structural complexity that, for each distinct patch (continuous area of one biotope class within a landscape), divides the ratio of patch perimeter by the minimum perimeter possible for a maximally compact patch (a single raster square) of the corresponding patch area (McGarigal et al., 2002). The Shape Index for each biotope class was then averaged to give an overall measure of landscape complexity. When the shape Index equals one, all patches within the landscape are maximally compact, whilst higher Shape Indices characterize more complex shapes of biotope patches (Forman, 1995, McGarigal et al., 2002). |
| Uncropped connectance index | A measure of functional habitat connectivity that equals the number of functional joinings between patches of uncropped land (patches within <25 m of each other using Euclidean distance) divided by the total number of possible joinings between all patches of uncropped land, then multiplied by 100 to convert to a percentage (McGarigal et al., 2002). An index score of zero is obtained when either there is a single patch of uncropped land or none of the patches of uncropped land are "connected", whereas an index score of 100 is obtained when every patch of uncropped land is "connected" (McGarigal et al., 2002). |

SHBDI and shape index are measures of landscape complexity, and the uncropped connectance index is a measure of functional connectivity between areas of semi-natural

habitat (McGarigal et al., 2002). Landscape complexity and the connectivity of semi-natural habitats were deemed as important aspects to investigate because they have been found to exert a strong influence on farmland invertebrate populations (Weibull et al., 2000, Steffan-Dewenter, 2003, Weibull et al., 2003, Albrecht et al., 2007, Diekotter et al., 2008, Meyer et al., 2009, Chaplin-Kramer et al., 2011, Shackelford et al., 2013, Steckel et al., 2014, Perovic et al., 2015, Rossetti et al., 2017). SHBDI and shape index were selected as they measure different aspects of landscape complexity (Table 2.3): SHBDI is a measure of compositional complexity (*e.g.* SHBDI increases when landscapes are composed of a greater number of biotopes and/or the proportional distribution in area between different biotopes becomes more equitable), whereas shape index is a measure of structural complexity (*e.g.* shape index increases as biotope patch shapes become more complex) (McGarigal et al., 2002, Fahrig et al., 2011).

The uncropped connectance index measures the functional connectivity between patches of semi-natural habitat within a landscape (*e.g.* uncropped connectance index scores increase as the number of functional joinings between patches of uncropped land increase) (Tischendorf and Fahring, 2000, McGarigal et al., 2002, Hein et al., 2004). When measuring the connectance index between patch types within Fragstats, the user must set a threshold distance (in metres) below which patches are deemed functionally connected (McGarigal et al., 2002). Here, the threshold distance was set at 25 m for two reasons. Firstly, setting it below 25 metres resulted in connectance index scores of zero within a high proportion of landscapes. Secondly, most groups of invertebrates investigated during this study (*e.g.* Araneae, Coleoptera, Diptera, Hymenoptera and Lepidoptera) can easily disperse between patches of semi-natural habitat separated by 25 metres (Coombes and Sotherton, 1986, Shreeve, 1995, Sommaggio, 1999, Thomas et al., 2003, Wratten et al., 2003, Holland et al., 2004, Cant et al., 2005, Knight et al., 2005, Osborne et al., 2008a, Zurbuchen et al., 2010). For these invertebrate groups, patches of uncropped land separated by up to 25 metres are 'functionally', rather than 'physically', connected (Tischendorf and Fahring, 2000, Uezu et al., 2005, Baguette and Van Dyck, 2007, Dennis et al., 2013, Severns et al., 2013). During all Fragstats analysis, a four-cell neighbourhood rule was selected instead of a nine-cell neighbourhood rule because it provides greater detail (*i.e.* higher spatial resolution) (McGarigal et al., 2002).

Distances between margin plots within each study farm ranged between 0.04 and 1.96 km (mean distance ± SEM: 0.62 ± 0.03 km). Consequently, landscape radii surrounding each margin plot often overlapped at all spatial scales (Figure 2.6). This could potentially be considered as pseudo-replication and should be borne in mind when interpreting the results of landscape analysis. However, Fuentes-Montemayor et al. (2011) found that the effect of

landscape composition on farmland moth populations was largely unchanged when data from overlapping radii was included within the analysis.

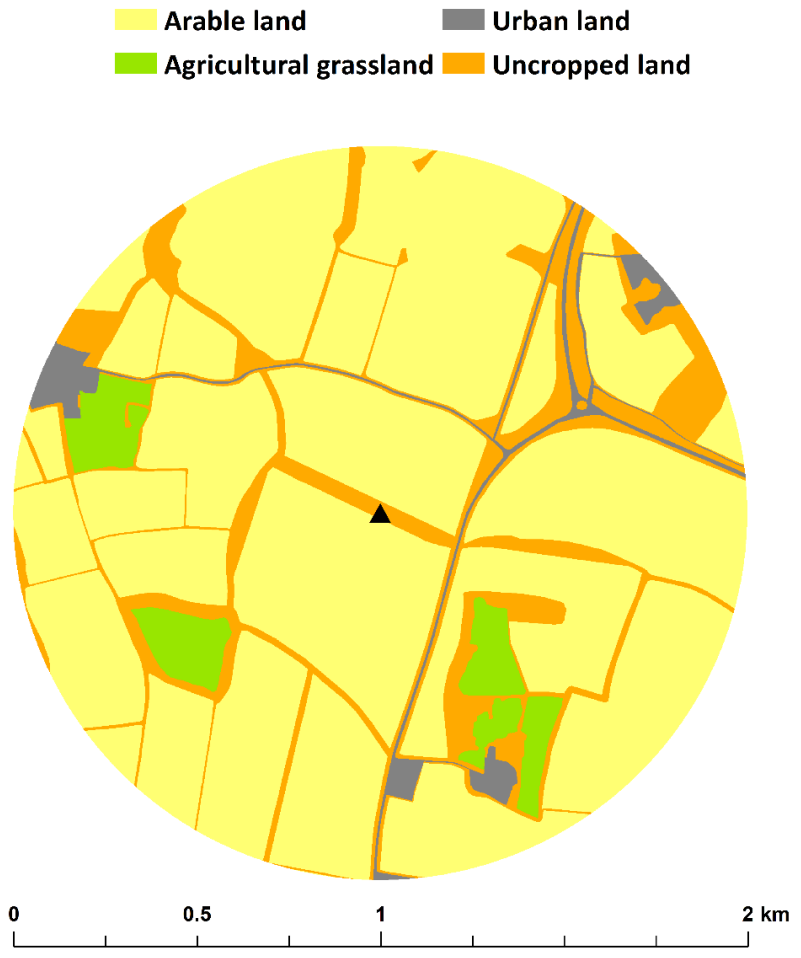


**Figure 2.5.** A biotope raster map example created in ArcGIS (raster squares set at 0.5 x 0.5 m). In this example biotopes are mapped within a 1 km radius centred on an individual margin plot (black triangle).

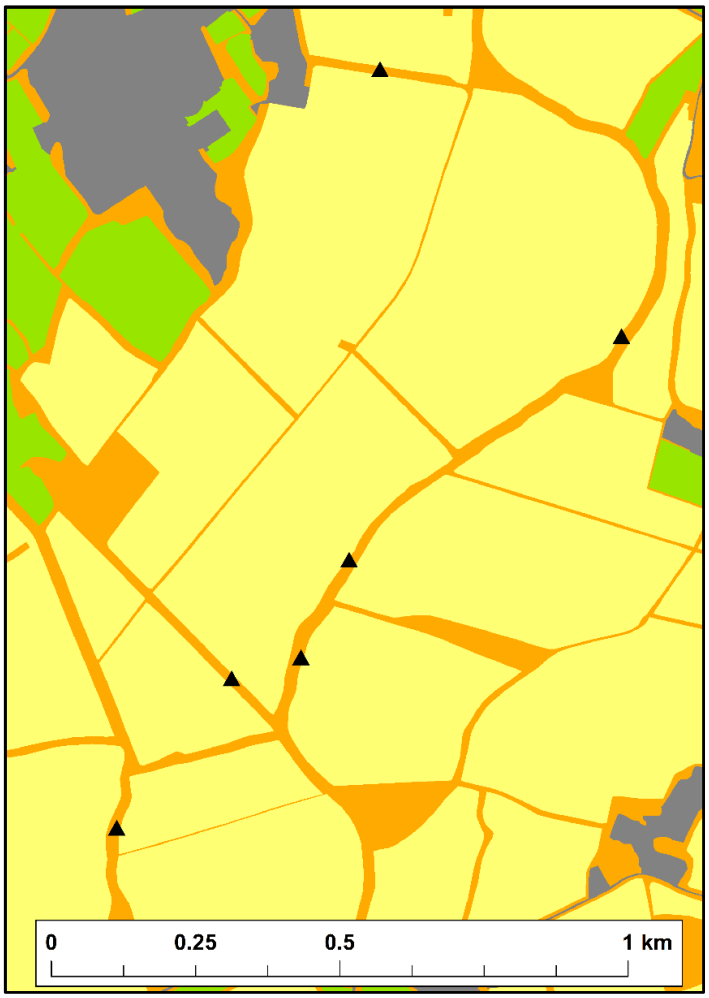


**Figure 2.6.** An example of how individual margin plots (black triangles) were distributed within a single study farm. Note that in most cases the distance between margin plots does not exceed 1 km and can be as little as < 250 m. This example includes field margin plots within study farm 16, Old Park Farm, Much Hadham, Hertfordshire (TL 44319 16007).

## 2.4 Measurement of soil-based services

### *2.4.1 Soil carbon, nitrogen and organic matter*

Field margin soil carbon, nitrogen and organic matter pools were quantified by collecting three soil samples positioned at 25, 50 and 75 metres along the centre of each 100 m plot (Figure 2.7). Samples were collected in September 2014 using a 6 cm deep (6.30 cm diameter) soil core.

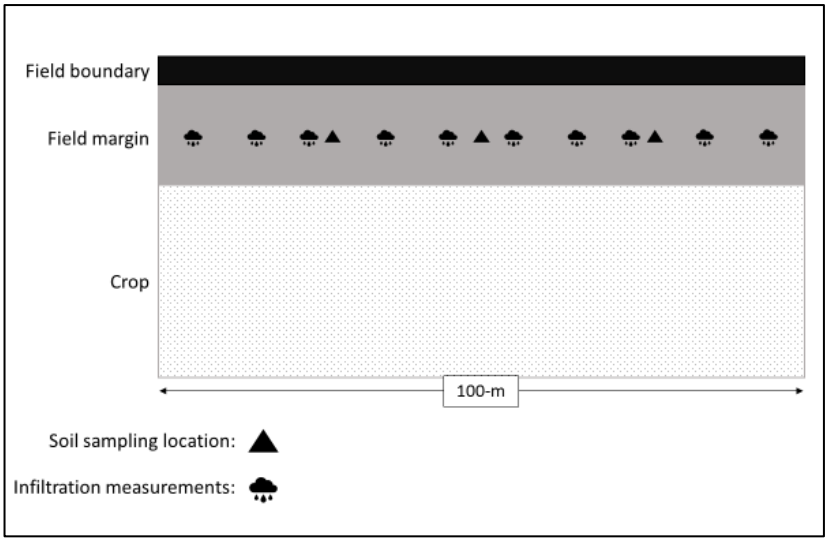


**Figure 2.7** Schematic diagram showing soil sampling and infiltration measurement locations within each field margin plot.

During collection, vegetation and surface litter was removed before each soil sample was taken. After collection, all roots and stones > 3mm in diameter were removed from each soil sample by hand sorting and sieving (2.8 mm mesh). Soil samples were then oven dried at 60°C until constant weight and weighed. The volume of stones and roots found within each soil core was then measured by volume displacement and subtracted from the core volume to obtain the field volume of each soil sample. Soil bulk density was then calculated using the following formula:

$$D_b = \frac{M_d}{V}$$

Where $D_b$ is soil bulk density (g C $cm^3$), *Md* is the mass (g) of the oven dried soil and *V* is its field volume ($cm^3$). Total soil nitrogen and soil carbon concentrations (%) were determined by taking subsamples from each oven dried soil sample, grinding them to a fine powder using a ball mill and analysing them using an Elementar Vario EL elemental analyser (Hanau, Germany). Soil carbon and nitrogen stocks per unit area (kg $m^{-2}$ soil) were then calculated for each soil sample using carbon and nitrogen concentrations and bulk density measurements.

The Organic matter content of individual soil samples was analysed using the loss on ignition method, whereby the loss in mass is recorded after being exposed to temperatures up to 560oC for nine hours. A subsample of soil from each core was placed in a crucible and its mass was recorded. Crucibles were then put into a furnace with a starting temperature of 100 °C.

The heat was then increased to 560 °C by increasing the temperature in 100 °C increments every thirty minutes (*e.g.* 100, 200, 300, 400, 500, 560 degrees). Once at 560 °C samples were left for six hours before they were reweighed, and the end mass was subtracted from the original mass to get the organic matter content. Organic matter content (%), carbon stocks per unit area (kg C $m^{-2}$ soil) and nitrogen stocks per unit area (kg C $m^{-2}$ soil) were determined for each individual sample and values were averaged across the three samples from each margin plot. Lab analysis revealed that soil carbon pools within field margins at study farm 13 were all statistical outliers (Figure 2.8). Consequently, samples from study farm 13 were excluded from soil carbon data analysis.

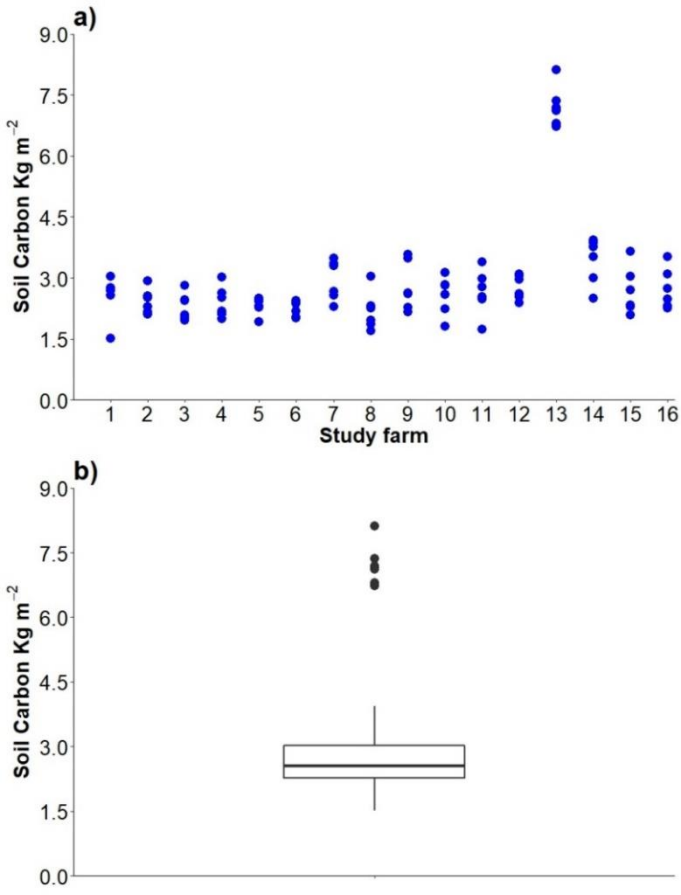


**Figure 2.8.** Showing (a) a scatterplot of field margin soil carbon pools (kg $m^{-2}$) across the 16 study farms and (b) a boxplot of field margin soil carbon pools (kg $m^{-2}$). The graphs clearly show that the soil carbon values from within field margins at site 13 are outliers.

*2.4.2 Soil rainfall infiltration*

The simplified falling-head (SFH) technique was used to assess the soil rainfall infiltration rate within individual field margin plots as a proxy measurement of flood alleviation potential. This method enables the rapid determination of soil saturated hydraulic conductivity ($K_{fs}$) within the field (Bagarello et al., 2004, Angulo-Jaramillo et al., 2016), and yields statistically similar results to more complex techniques, such as the pressure infiltrometer (Bagarello et al., 2012). A single ring of known diameter *A* [mm] (95 mm) was inserted into the soil to a depth of 0.03 m to ensure that the area of soil receiving the application of water was enclosed (Angulo-Jaramillo et al., 2016). Vegetation where the ring was inserted into the soil was trimmed as close to the soil surface as possible and any surface residue was removed (*ibid*). Also, when the ring was driven into the soil the sides were kept vertical to keep soil disturbance to a minimum (*ibid*) (Figure 2.9). A known volume of water *V* [L] (0.24 litres) was then applied to the soil surface enclosed by the inserted ring and the time $t_a$ from when the water first hit the soil surface until it had completely infiltrated was recorded (*ibid*). Soil moisture content was measured before (just outside the infiltration ring) and after (within the infiltration ring) water application using a soil moisture probe. Soil $K_{fs}$ (mm $h^{-1}$) was then calculated with the following equation taken from Bagarello et al. (2004):

$$K_{fs} = \frac{\Delta 0}{(1-\Delta 0)t_a}\left[\frac{D}{\Delta 0} - \frac{\left(D+\frac{1}{\alpha *}\right)}{1-\Delta 0}\, ln\left(1+\frac{(1-\Delta 0)D}{\Delta 0\left(D+\frac{1}{\alpha *}\right)}\right)\right]$$

Where Δθ is the difference between the saturated water content inside the cylinder, $\theta_{fs}$ ($L^3\,L^{-3}$), and initial water content outside the cylinder, $\theta_i$ ($L^3\,L^{-3}$). $D = V / A$ (L) is the depth of water in the ring at the beginning of measurement and $\alpha^*$ is the saturation potential coefficient for $K_{fs}$ (Elrick et al., 1989). A saturation potential coefficient $\alpha^*$ for each margin plot was estimated based on the soil type present (Elrick et al., 1989). A total of 10 replicate measurements were made at 10 m intervals, between five and 95-m along each along the centre of each field margin plot (see Figure 2.7 in §2.4.1). The ten measurements per margin plot were averaged for analysis. Infiltration measurements were carried out during April 2017.

**Figure 2.9** Showing the infiltration ring inserted into the soil surface.

### 2.5 Measurement of insect mediated services

Pollination and pest control services were assessed during 2016 by conducting assays within the adjacent crop alongside eight paired high and low quality margins across eight study farms. Two margin pairs were in different fields and six margin pairs were within the same field. The crops in the adjacent fields were either spring wheat, winter wheat or winter barley. Cropping was standardised for the two margin pairs that were situated in different fields. All fields were under conventional management, but no insecticide applications took place during pollination or pest control assays.

Within each experimental field, pest control and pollination services were measured at two distances from the field margin: the outer five metres of the crop (hereafter the 'crop edge') and 20 metres into the crop (hereafter the 'crop interior'). These locations were chosen as a compromise between logistics and the ability to detect treatment effects (high vs low quality) on ecosystem service spill-over into the adjacent crop. Logistically, adding a third location further into the crop (*e.g.* at 50 metres) would have required an extra 144 strawberry plants and 768 sentinel prey cards, which would have exceeded the space (greenhouse and transport space available for strawberry plants) and time (preparation and collection of sentinel prey cards) allocations allotted to these experiments. Moreover, the outer five metres of the crop and 20 metres into the crop are easily accessed by the sterile strip/margin and first vehicle tramline, respectively.

In terms of detecting a treatment mediated spill-over effect, pollination and pest control services tend to decline rapidly as you move into the crop regardless of the floral abundance and richness of the adjacent margin (Tschumi et al., 2016a, Tschumi et al., 2016b, Woodcock et al., 2016a). Nevertheless, previous studies have detected treatment effects of flower-rich margins on pest control and pollination at 10, 25 and 50 metres into the adjacent crop (*ibid*). Given these findings, and the logistical constraints outlined above, the outer five metres and 20 metres into the crop were deemed appropriate locations to measure the pest control and pollination services flowing from the high and low quality margins used in this study.

*2.5.1 Pollination*

Pollination services were assessed using strawberry (*Fragaria x ananassa*) phytometers placed within the crop adjacent to field margin plots. Strawberries were selected over other species for five reasons: (1) they are easy to cultivate and keep healthy in relatively small pots; (2) they are an economically important crop within the UK (DEFRA, 2014); (3) they are an aggregated fruit so pollination success can be measured on each strawberry independent of total fruit set and the covariates that influence this (Andersson et al., 2012); (4) a wide range of insect taxa visit strawberry flowers owing to their open flower structure (Nye and Anderson, 1974, Klatt, 2013); and (5) although strawberries are to a certain extent self-compatible, insect pollination increases yield, quality, shelf-life, the number of fertilised achenes and reduces the number of malformations (Free, 1993, Dimou et al., 2008, Klatt et al., 2014).

The mid-season variety 'Cambridge Favourite' was selected because it is hardy, produces large amounts of flowers and has excellent disease resistance. A total of 288 strawberry Frigo-plants (frozen first year plants with exposed bare roots) were placed in individual 1 L pots with 1 L of John Innes N$^{o}$ 2 compost and 2 g of p4 polymer (Broadleaf P4) to ensure that nutrients and water would not be a limiting factor whilst exposed to pollination in the field. Plants were established in a pollinator free glass house in early April and left to develop until flowering. Once in bud, the plants were exposed to pollination in the field between May 14$^{th}$ and June 5$^{th}$. Flowering was timed to coincide with winter oilseed rape (*Brassica napus*) flowering to assess the pollination services provided next to high and low quality field margins during this period. However, it is important to note that, whilst the pollinator communities that visit strawberry and oilseed rape do show some overlap in the UK, they are not identical (Rader et al., 2016). Arrays of three strawberry phytometers were

placed at 25, 50 and 75 metres along each margin plot at two positions: the crop edge and the crop interior (the outer five metres of the crop and 20 metres into the crop, respectively), giving 18 phytometers in total adjacent to each margin plot (Figure 2.10). Phytometers were put out in arrays of three to ensure cross-pollination and within an array plants were positioned just far enough away from each other to prevent flowers coming into physical contact (Andersson et al., 2012). To reduce water loss, pots were dug halfway into the ground and were watered once in the field after seven days. Each array was enclosed by 50 mm wire mesh secured by bamboo canes to provide protection from grazing animals such as rabbits and deer, while allowing access to pollinating insects.

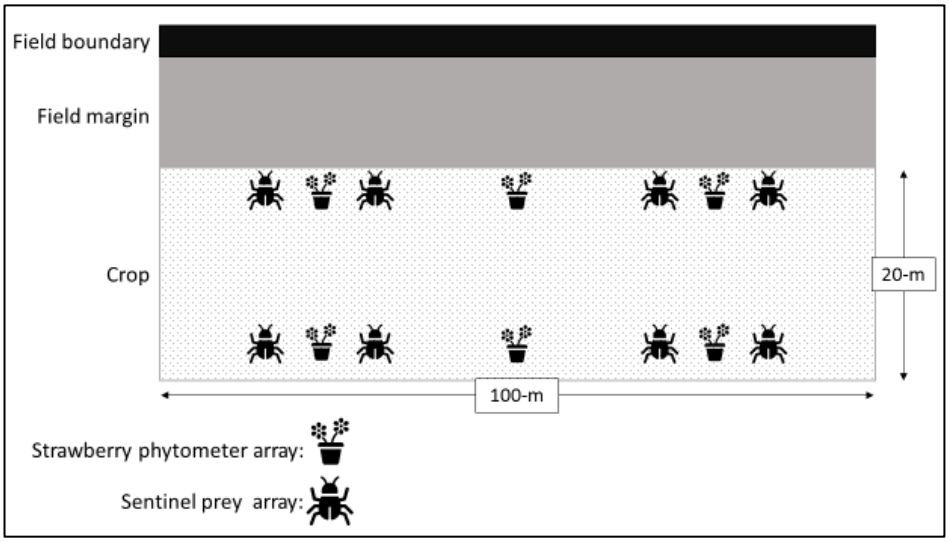


**Figure 2.10.** Schematic diagram showing the location of strawberry phytometer and sentinel prey arrays.

After two weeks of exposure, phytometers were collected and stored in a pollinator-free glass house to allow fruits to mature; during this period, any new flower buds were removed (Orford et al., 2016). When ripe, all strawberry fruits produced were weighed (g) and the height and width (cm) were measured using a Vernier calliper. Pollination success was measured on each fruit by counting the number of fertilised achenes, which is a direct measure of pollination success (Albano et al., 2009, Klatt et al., 2014). To establish the number of fertilised achenes produced, each fruit was blended in 100 ml of distilled water for exactly two minutes. Fertilised achenes are heavier so they sink to the bottom; whereas, unfertilised achenes are lighter and float on the water surface (Klatt et al., 2014). Unfertilised achenes were removed and then the number of fertilised achenes were counted. Depending on analysis, the number of fertilised achenes per fruit were either averaged at each crop position

or across both crop positions. Also, yield was calculated by summing the number of fruits produced at each crop position or across both crop positions.

*2.5.2 Pest control*

The level of pest control was assessed by conducting sentinel prey assays within the crop adjacent to margin plots. Sterilised moth eggs (*Ephestia kuehniella*) and fly larvae (*Calliphora vomitoria*) were used as sentinel prey to provide a proxy measure of the pest control services flowing from high and low quality field margins into the adjacent crop (Holland et al., 2017a). Fresh sterilised *E. kuehniella* (4 days old or less) eggs were supplied by Koppert BV (The Netherlands) and stored in a freezer before being used during the field assays. Live *C. vomitoria* larvae were purchased from local fishing tackle shops the day before each assay and stored in a fridge until required. A standardised number of *Ephestia* eggs (685.53 ± 9.04; mean ± SEM) were mounted onto a 5 x 2 cm white Drystick card (OECOS) within an exposed area of 1 $cm^2$ (0.5 x 2 cm) (Figure 2.11a), and four *Calliphora* larvae were live-pinned through the posterior end to a 5 x 2 cm strip of white plastazote (Figure 2.11b). Sentinel prey cards were exposed to predation during three assays conducted between the 19$^{th}$ of June and the 24$^{th}$ of July to cover the period where pests of spring and winter cereals are most active (AHDB, 2014).

During each assay, one card of each prey type was fixed in the crop canopy and one of each prey type on the ground at four locations within the crop edge (outer 5 metres of the crop) and crop interior (20 metres into the crop) situated at 15, 30, 70 and 85 metres running parallel to each 100 m field margin plot (Figure 2.10; §*2.5.1*). Cards fixed within the crop canopy were attached to the underside of the flag leaf of a random wheat or barley plant using a paperclip (Figure 2.11a). Cards attached to the floor were fixed in place using 38 mm length pins and placed next to each other at each sampling point. They were then covered with 13 mm wire mesh to prevent the entry of small mammals, birds and amphibians, whilst allowing access to predatory invertebrates (Figure 2.12) (Meek et al., 2002).

Sentinel prey cards were exposed for 24 hours before being collected. On collection, cards were scored on a five-point scale: zero = 0% eggs lost, or no larvae predated; one = 1 – 25% eggs lost or one larvae predated; two = 26 – 50% eggs lost or two larvae predated; three = 51 – 75% eggs lost or three larvae predated; and, four = 76 – 100% eggs lost or four larvae predated. Fly larvae were considered predated if they were not present on the card or if the contents had been consumed (e.g. by predators with piercing and sucking mouthparts). Pest control scores for each prey type were summed across the three assay rounds for each crop

position and height: crop edge ground, crop edge canopy, crop interior ground and crop interior canopy. These scores were then divided by the total predation score possible at each position and height to give a predation index between 0-1. However, for certain analyses predation indices were calculated using predation scores summed across crop positions. Calculation of predation indices revealed that the majority of moth egg and fly larvae cards placed on the ground adjacent to high and low quality margins received full predation (Figure 2.13). Consequently, ground-level predation data was excluded from subsequent data analysis.


**Figure 2.11.** Moth egg and fly larvae sentinel prey cards attached to the underside of the flag leaf of an individual wheat plant.

**Figure 2.12.** Moth egg and fly larvae sentinel prey cards attached to ground within the crop.

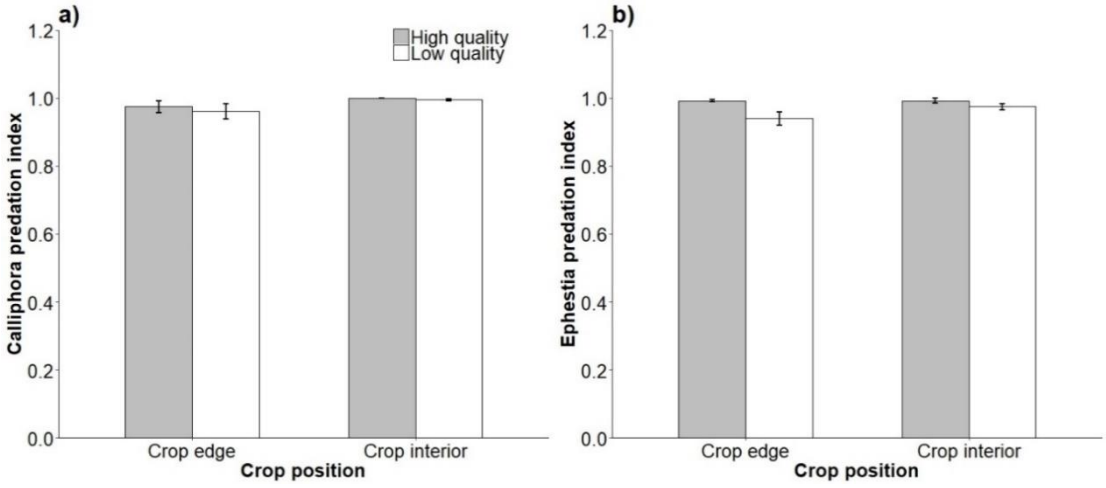


**Figure 2.13.** Showing mean (± SEM) predation index scores for (a) *Calliphora* larvae and (b) *Ephestia* eggs placed on the ground adjacent to high and low quality margin plots at the crop edge and crop interior.

## 2.6 Measurement of Biodiversity and ecosystem service providers

Pitfall trapping, line transects, and sweep netting were employed to assess the abundance and richness of invertebrate communities utilising field margins and the adjacent crop. All invertebrates collected were identified to either order, sub-order, family, morpho-species or species depending on whether the taxonomic group was used to assess the biodiversity or the abundance of ecosystem service providers. To assess biodiversity, invertebrate richness was calculated using the taxa divisions listed in Table 2.4. The invertebrate ecosystem service providers investigated included crop pests, crop pollinators and natural enemies. The taxa included in each of these groups is also listed in Table 2.4 below.

**Table 2.4.** Showing (a) the taxa used to calculate invertebrate richness during each survey and (b) the invertebrate taxa included in crop pest, crop pollinator and natural enemy ecosystem service provider groups.

*a) Taxa used to calculate invertebrate richness*

| | | | | |
|---|---|---|---|---|
| Acari | Carabidae | Dolichopodidae | Oedemeridae | Sepsidae |
| Agromyzidae | Cephidae | Dryomyzidae | Opiliones | Sialidae |
| Andrenidae | Cerambycidae | Elateridae | Opomyzidae | Sphaeroceridae |
| Anisoptera | Cercopidae | Empididae | Orthoptera | Sphecidae |
| Anthocoridae | Chalcidoidea | Formicidae | Pallopteridae | Staphylinidae |
| Anthomyzidae | Chironomidae | Halictidae | Panorpidae | Stratiomyidae |
| Aphididae | Chloropidae | Ichneumonidae | Pentatomoidea | Syrphidae |
| Apidae | Chrysomelidae | Isopoda | Phoridae | Tabanidae |
| Araneae | Chrysopidae | Lauxaniidae | Pipunculidae | Tenthredinidae |
| Asilidae | Cicadellidae | Lepidoptera | Platystomatidae | Tephritidae |
| Asteiidae | Coccinellidae | Lonchopteridae | Psyllidae | Thysanoptera |
| Baetidae | Collembola | Megachilidae | Pyrochroidae | Tingidae |
| Bibionidae | Conopidae | Melyridae | Rhopalidae | Tipulidae |
| Bombyliidae | Culicidae | Miridae | Scathophagidae | Ulidiidae |
| Braconidae | Curculionoidea | Muscidae | Scatopsidae | Vespidae |
| Bruchidae | Cynipidae | Mycetophilidae | Sciaridae | Zygoptera |
| Calypterate Diptera[1] | Delphacidae | Nabidae | Sciomyzidae | |
| Cantharidae | Dermaptera | Nitidulidae | Scraptiidae | |

*(b) Invertebrate taxa included in crop pest, crop pollinator and natural enemy groups*

| Crop pests[2] | | Crop pollinators[3] | Natural enemies[2] | |
|---|---|---|---|---|
| Aphidae | Elateridae | Andrenidae | Anthocoridae | Empididae |
| *Autographa gamma* | Miridae | *Apis mellifera* | Araneae | Formicidae |
| Bruchidae | Nitidulidae | *Bombus* spp. | Asilidae | Opiliones |
| Cephidae | Opomyzidae | Halictidae | Cantharidae | Nabidae |
| Chloropidae | *Pieris brassicae* | Megachilidae | Carabidae | Neuroptera |
| Chrysomelidae | *Pieris rapae* | Calypterate Diptera[1] | Chilopoda | Parasitoid wasps |
| Cicadellidae | Thysanoptera | Scathophagidae | Coccinellidae | Scathophagidae |
| Curculionoidea | Tipulidae | Syrphidae | Dolichopodidae | Staphylinidae |
| | | | | Syrphinae |

[1] Excludes Scathophagidae

[2] Based on information provided within AHDB (2014)

[3] Based on information provided within Rader et al. (2016)

Certain invertebrate taxa were included in several ecosystem service groups due to differences between larval and adult feeding modes or because several feeding modes were exhibited in either the adult or larval stage. For example, hoverflies belonging to the sub-family Syrphinae were considered as natural enemies and pollinators because the larvae feed on aphids but the adults visit flowers to feed on nectar and pollen (Rotheray and Gilbert, 2011). Table 2.1 in §2.1 lists the number of margin plots used for each invertebrate survey method.

Before detailing the methodologies used during pitfall trapping, sweep netting and line transects, it is important to highlight the shortcomings of each of these survey techniques and how these shortcomings influence data interpretation. Firstly, it has long been established that pitfall trap catches are strongly biased by vegetation structure, body size, population density and invertebrate activity (Adis, 1979, Thomas et al., 1998, Melbourne, 1999, Lang, 2000). Secondly, sweep netting catches are biased towards heavier individuals that are active near the tips of the vegetation (Ausden and Drake, 2006, Doxon et al., 2011). Thirdly, line transects are biased towards more conspicuous and/or larger flying insects (Ausden and Drake, 2006). Moreover, differences between transects in the numbers of flower-visiting insects recorded are largely determined by differences in floral resources (Holland et al., 2013, Holland et al., 2015, Wood et al., 2015a).

Given these biases, all three survey techniques should be viewed as measures of invertebrate activity/habitat attractiveness, rather than measures of relative abundance. Therefore, the use of pitfall trapping, sweep netting and line transects makes it difficult to detect population level responses of invertebrate groups, especially given that surveys were conducted over a single survey season and a before-after control-impact approach was not used (Kleijn et al., 2006, Scheper et al., 2015). Nonetheless, population level responses can still be inferred from these survey methods if they are combined with behavioural observations. For example, if larger numbers of feeding bumblebees are recorded in forb-rich compared to forb-poor biotopes during transects (*i.e.* increased activity and resource use), then flower rich biotopes can be considered to have high attractiveness owing to their increased nutritional value (Wratten et al., 2012). Due to the importance of floral resources for bumblebee colony survival and production (Kamper et al., 2016), forb-rich biotopes should therefore enhance bumblebee populations across the landscape providing other habitat resources are not limiting (*e.g.* lack of nesting habitat) (Roulston and Goodell, 2011, Sardinas et al., 2016). In addition, the level of ecosystem services provided by invertebrate groups such as pollinators and natural enemies is often positively correlated with increased activity (*e.g.*

yield and pollinator visitation rate) (Bartomeus et al., 2014, Woodcock et al., 2016a). This suggests measurements of invertebrate ecosystem service provider activity should allow valid inferences to be made about the ecosystem service potential of different field margin plots.

*2.6.1 Pitfall trapping*

Pitfall traps were used to assess the abundance and richness of epigeal invertebrates within field margin plots. Each trap consisted of a 0.33-L plastic pot (7.5 cm in diameter and 10.8 cm depth) buried in the ground so that the lip of the pot was flush with the soil surface (Ausden and Drake, 2006). Pots were filled with 0.15-l of NaCl solution and a few drops of colourless and odourless detergent (Wilkinsons pet friendly washing-up liquid) to reduce surface tension (*ibid*). Plastic rainfall covers (90 mm diameter) were set approximately 5 cm above each pitfall to prevent the overflow of trap contents but allow entry of invertebrates (Meek et al., 2002). Three pitfall traps were set at 25, 50 and 75 metres along the centre of each 100-m margin plot (Figure 2.9).

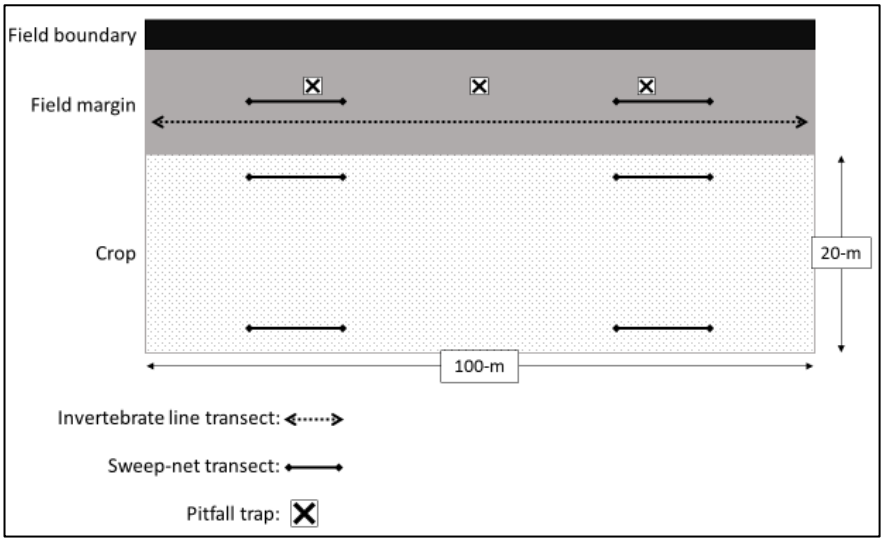


**Figure 2.14.** Schematic diagram showing the location of invertebrate line transects, sweep net transects and pitfall traps within each 100 m margin plot.

Traps were operational for seven days during the beginning of June 2015 (weeks 22 and 23), with traps within a site being set on the same day. On collection trap contents were stored in 70% ethanol for later identification under a binocular microscope. The three traps per margin plot were pooled for data analysis. The abundance of crop pests and natural enemies, and invertebrate taxonomic richness were then calculated for each margin.

*2.6.2 Transects*

The abundance and richness of aerial invertebrates were assessed using standardised line transect walks (Ausden and Drake, 2006). A transect of 100 metres in length was marked out along the centre of each field margin plot (Figure 2.14; §2.6.1). Walking at a standard pace, all visible invertebrates >3mm were recorded within a two-metre corridor (flower-visiting and non-flower-visiting insects). Transects were walked four times during 2016 within two discrete periods: twice between May 14$^{th}$ –and June 9$^{th}$ (early season) and twice between July 15$^{th}$ and August 23$^{rd}$ (late season). As far as possible, the UK Butterfly Monitoring guidelines for transects were adhered to: surveys were conducted between 0930 and 1700 h when the temperature is above 13 °C with at least 60% clear sky, or above 17 °C with any level of cloud and wind speeds were < 14km/hr (Pollard and Yates, 1994). Any invertebrates that could not be identified in the field were collected, stored in 70% ethanol and identified in the lab. For flower-visitors recorded during transects, it was noted whether they were feeding (*e.g.* taking nectar or pollen from a flower) and what species of flower they were observed feeding on. These data were collected to assess differences in habitat attractiveness between high and low quality margin plots, and to determine flower preferences for important flower-visiting taxa.

After each transect walk field margin floral resources were estimated within the same 2 x 100 m corridor where invertebrates were surveyed. A simple floristic index was used to record flower abundance: 1, 1–25 flowering units; 2, 26–200 flowering units; 3, 201– 1000 flowering units; 4, 1001–5000 flowering units; and 5, >5000 flowering units (Carvell et al., 2007). One flowering 'unit' was counted as a single flower (*e.g. Rubus fruticosus*), an umbel (*e.g. Heracleum sphondylium*), head (*e.g. Trifolium repens*), spike (*e.g. Rhinanthus minor*) or capitulum (*e.g. Centaurea nigra*) (*ibid*). Due to the importance of Poaceae pollen to many hoverfly and other Dipteran species (Wäckers et al., 2007), the number of Poaceae floral units were also recorded during flower surveys, with one flowering unit consisting of a single panicle or spike. During analysis, floristic index scores for each species recorded within each margin

plot were converted into the corresponding interval median value for each range: 1 = 13 flowers; 2 = 113 flowers; 3 = 600·5 flowers; 4 = 3000·5 flowers; 5 = 15000 flowers (Carvell et al., 2007).

Invertebrate data from transects was used to calculate several biodiversity and ecosystem service provider metrics. The biodiversity metrics calculated included: day-flying Lepidoptera abundance and richness; bumblebee abundance and species richness; hoverfly abundance and species richness; and, invertebrate taxonomic richness (using the taxa listed in Table 2.4 above). *Bombus terrestris* and *Bombus lucorum* were recorded collectively due to the difficulty of separating the workers of these species in the field (Falk, 2015). Also, all hoverflies were recorded to species apart from *Melanostoma* spp., grey *Platycheirus* spp., orange *Platycheirus* spp. and *Sphaerophoria* spp. Furthermore, if a bumblebee or hoverfly was observed but could not be identified in the field or caught for later identification, it was recorded as a bumblebee or hoverfly 'in flight' and included within abundance counts for each group (Croxton et al., 2002). The ecosystem service provider metrics recorded during transects included the abundance of crop pests, crop pollinators and natural enemies. Depending on the type of analysis, invertebrate biodiversity, ecosystem service provider, behaviour and flower data was either pooled across all transect surveys or pooled within the two survey seasons: early and late.

*2.6.3 Sweep netting*

To assess the canopy-active invertebrates that were active during the sentinel prey experiments, two rounds of sweep netting were carried out between the 25th of June and 24th of July 2016. Owing to logistics, ground dwelling invertebrates could not be sampled. However, recent work suggests that it is the canopy active predators that provide the largest contribution to control of crop pests that are mostly active in the crop canopy (Holland et al., 2012, Woodcock et al., 2016a). Invertebrates were collected at three positions: the margin, the outer five metres of the crop (crop edge) and 20 metres into the crop (crop interior). At each position 30 sweeps with a 30 cm diameter canvas sweep net were made along two separate 15 m transects running parallel to the field boundary. Transects were positioned between 15-30 and 70-85 metres along each 100 m field margin plot (Figure 2.14).

Sampling only took place between 1000 – 1500 during dry conditions when wind speeds were <15 km/hr, temperatures were >17$^{o}$C and the vegetation was dry (Doxon et al., 2011). Transects were walked at a constant pace (<8 km/hr) and care was taken to sweep only

the upper 25% of the vegetation in an arc approximately 2 m wide (Buffington and Redak, 1998). To minimize the escape of collected invertebrates, the net was twisted 180° at the end of each sweep arc (Doxon et al., 2011). Sweeping was synchronized with walking so that when a step was taken a single sweep was made. This meant that exactly 15 sweeps were made per transect section and a total of 30 sweeps at each position. After each transect section, the sweep net was closed off at the top with one hand and the side of the canvas was knocked with the other hand to ensure that the invertebrates collected at the bottom of the net (*ibid*). The net contents were then emptied into a sealable plastic freezer bag. Samples were frozen until later identification in the lab whereby the abundance of crop pests and natural enemies, and invertebrate taxonomic richness were calculated for each margin. Depending on analysis, sweep net data was either summed across survey rounds at each survey position (margin, crop edge, crop interior) or summed across survey rounds and survey positions.

**2.7 Margin environmental and management data**

To achieve research objective five, *"to establish the key drivers (both local and landscape) promoting ecosystem service provision and invertebrate biodiversity within arable field margins"*, a range of additional local management/abiotic/biotic data was collected. The variables that were measured, along with the timing of measurements and surveys that each variable relates to are listed in Table 2.5 below.

**Table 2.5.** Additional margin (a) management, (b) abiotic and (c) biotic variables measured within and adjacent to each 100 m field margin plot.

| Management and environmental variables | Description | Relevant survey data[1] |
|---|---|---|
| *a) Management variables:* | | |
| Margin seed mixture | Whether the margin plot was created by: sowing a grass only seed mixture (grass mix); sowing a seed mix that included flowers (flower mix); or, left to naturally regenerate (nat regen). This information was gathered from farmers/land owners during 2014. | All |
| Margin cutting frequency | The number of times per year each field margin plot is cut. If a margin was cut once every two or three years it would be given a score of either 0.5 or 0.3, respectively. This information was gathered from farmers/landowners during 2014. | All |
| Margin cuttings | Whether the cuttings were left *in situ* (left) or removed (removed). This information was gathered from farmers/landowners during 2014. | All |
| Crop sowing date | Whether the cereal crop in the field adjacent to each margin plot was winter (0) or spring (1) sown. This information was gathered from farmers/landowners during every year of the study. | Pol, Pest, Trn, Swp |
| *b) Abiotic variables* | | |
| Margin soil type | Determined in the field during soil sample collection in September 2014. Field margin soils were either silt loam, clay loam or sandy loam. | *Kfs*, Om |
| Margin vehicle traffic | Determined in the field during soil infiltration measurements in April 2017. Vehicle use was estimated by classifying wheel rut depth: none, no visible wheel ruts or tyre tracks; light, vehicle tyre tracks on the surface but no wheel ruts evident; intermediate, shallow wheel ruts < 10 cm; heavy, deep wheel ruts > 10 cm. | *Kfs* |
| Margin bare ground | The mean percentage bare ground recorded within three 2 x 2 m quadrats. The percentage of bare ground was measured twice: once in June 2015 and once in May 2016. | Pol, Pest, Trn, Swp |
| Margin width | The mean width (in metres) of each field margin plot. Width was measured once during August 2014 at three points along each field margin plot: 25, 50 and 75 m. | Pol, Pest, Trn, Swp, *Kfs*, Om |

[1] All, all data collected; Pol, pollination data; Pest, pest control data; Trn, transect data; Swp, sweep net data; *Kfs*, soil infiltration data; Om, soil organic matter data.

**Table 2.6.** Continued

| Management and environmental variables | Description | Relevant survey data[1] |
|---|---|---|
| *c) Biotic variables* | | |
| Margin vegetation height | Measured using a 30 cm diameter drop disk at six regular intervals along two diagonal transects within the three 2 x 2 m quadrats used during vegetation surveys (12 measurements per quadrat; 36 measurements per margin). Vegetation height was measured: twice during each transect survey season; twice during phytometer assays; and, twice during sweep net surveys/sentinel prey assays. | Pol, Pest, Trn, Swp |
| Length of adjacent hedge in flower | The length (in metres) of hedgerow in flower adjacent to each field margin plot measured: twice during each transect survey season; twice during phytometer assays; and, twice during sweep net surveys/sentinel prey assays. | Pol, Pest, Trn, Swp |
| Crop weediness | The weediness of the crop adjacent to each field margin plot. Weediness was measured using the following scale: 0, no weeds; 1, few weeds; 2, moderate weeds; 3, abundant weeds. This value is a mean of eight measurements taken at 15, 30, 70 and 85 metres within the crop edge and crop interior adjacent to each 100 m field margin plot. Measurements were taken twice: once during phytometer assays and once during pest control assays in 2016. | Pol, Pest, Swp |

[1] All, all data collected; Pol, pollination data; Pest, pest control data; Trn, transect data; Swp, sweep net data; *Kfs*, soil infiltration data; Om, soil organic matter data.

# Chapter 3: Do high quality field margins deliver ecosystem service and invertebrate biodiversity benefits more effectively than low quality field margins?

### 3.1 Introduction

The adoption of intensive farming practices have led to widespread declines in farmland biodiversity (Donald et al., 2001, Robinson and Sutherland, 2002, Benton et al., 2003, Donald et al., 2006, Firbank et al., 2008), the deterioration of agronomically important ecosystem services (Kremen et al., 2002, Zhang et al., 2007, Deguines et al., 2014), and the degradation of aquatic and terrestrial ecosystems (Matson et al., 1997, Tilman et al., 2002, Stoate et al., 2009, Tilman and Clark, 2015). To alleviate these impacts, agri-environment schemes (AES) were introduced across the European Union under the Common Agricultural Policy in 1986 (Whittingham, 2011, Batary et al., 2015). AES subsidise farming practices that increase biodiversity, enhance the landscape, and improve water, air and soil quality (Natural England, 2013a, b, 2018). One way to achieve these objectives within arable systems is through the creation and maintenance of field margins (Marshall and Moonen, 2002, Borin et al., 2010, Holland et al., 2013). Consequently, within the UK several different agri-environmental options for field margin management were developed and made available to farmers (Natural England, 2013a, b, 2018).

Field margins can provide a range of ecological and environmental benefits, such as habitat resources for wildlife in an otherwise resource-poor environment (Bence et al., 2003, Haenke et al., 2009, Lye et al., 2009, Scheper et al., 2015, Westbury et al., 2017), reducing agrochemical run-off and soil erosion into adjacent habitats (Kay et al., 2009, Borin et al., 2010) and supporting populations of agronomically important invertebrates (Holland et al., 2008, Holland et al., 2012, Wood et al., 2013, Blaauw and Isaacs, 2014a, 2015). But despite their potential multifunctionality, individual field margin options within AES were largely designed to fulfil a single ecological objective (Natural England, 2013a, b, 2018). The creation of forb-rich field margins is one such example. Dramatic reductions in farmland floral resources, due to agricultural intensification and expansion (Howard et al., 2003), is one of the principle drivers behind the long-term declines of insect flower-visitors across northern Europe (Biesmeijer et al., 2006, Potts et al., 2010, Wallisdevries et al., 2012, Carvalheiro et al., 2013, Ollerton et al., 2014, Goulson et al., 2015, Potts et al., 2015). By ameliorating the lack of floral resources on farmland, it is hoped that forb-rich field margins will help to reverse these declines (Goulson et al., 2015). Indeed, studies suggest that sowing forb-rich margins might achieve this objective, since, compared to floristically poor control areas, they support a greater abundance and richness of pollinators (Haaland et al., 2011, Scheper et al., 2013, Holland et al., 2015, Scheper et al., 2015) and, when implemented at the farm scale,

can increase the population size of bumblebees (*Bombus* spp.) (Carvell et al., 2015, Wood et al., 2015c, Carvell et al., 2017).

Beyond providing foraging habitat for flower-visitors, there is a growing body of evidence which suggests that forb-rich margins can also promote agronomically important ecosystem services (Wratten et al., 2012), such as crop pollination (Blaauw and Isaacs, 2014a), natural pest control (Woodcock et al., 2016a) and weed suppression (Smith et al., 1999). Typically, studies examining ecosystem service provision within forb-rich margins focus on a single service in isolation (Bommarco et al., 2013) and ignore the ecosystem disservices that margins might promote, such as supporting populations of crop pests (but see, (Eggenschwiler et al., 2013, Grass et al., 2016). Furthermore, studies in experimental grasslands have found positive relationships between the diversity of forbs, flood alleviation (via increased infiltration capacity) and climate change mitigation (via increased carbon storage) (De Deyn et al., 2011, Cong et al., 2014, Fischer et al., 2014, Fischer et al., 2015), but these relationships have yet to be tested within field margins. If it were demonstrated that forb-rich margins could enhance numerous agronomic and environmental benefits simultaneously, in addition to providing floral resources, then landowners would be more likely to adopt them (Bommarco et al., 2013); especially if ecosystem service provision was linked to agri-environmental payments that offset implementation and opportunity costs (Reed et al., 2014, Smith and Sullivan, 2014).

Whilst the broad aim of forb-rich margins is to enhance flower-visiting insect populations on farmland (Natural England, 2013a, b), in the UK, seed mixes were almost exclusively developed by studying bumblebees (Kells et al., 2001, Carvell et al., 2004, Pywell et al., 2005b, Carvell et al., 2006, Pywell et al., 2006, Carvell et al., 2007, Pywell et al., 2011). Consequently, seed mixes are dominated by important bumblebee forage species such as *Centaurea nigra, Centaurea scabiosa, Lotus corniculatus, Trifolium pratense,* and *Trifolium hybridum* (Carvell et al., 2007, Pywell et al., 2011). Worryingly however, a recent analysis of the dietary preferences of solitary bees on UK farmland showed that they collect most their pollen from plant species not included in AES seed mixes (Wood et al., 2016). This suggests that current AES will be unsuccessful in supporting pollinators other than bumblebees unless seed mixes are revised to cater for a wider-range of flower-visiting taxa. Failure to consider the foraging preferences of non-bumblebee pollinators may also limit the extent to which forb-rich margins provide secondary benefits to agriculture, such as natural pest control. For example, pollen and/or nectar can enhance the fecundity and longevity of flower-visiting natural enemies (Wäckers et al., 2005, Lee and Heimpel, 2008, van Rijn et al.,

2013), and their ability to control crop pests (Blaauw and Isaacs, 2012, Blaauw and Isaacs, 2015). But there is little overlap between the flower species utilised by natural enemy groups and bumblebees (Jervis et al., 1993, Campbell et al., 2012, Garbuzov and Ratnieks, 2014); and, apart from the single study by Wood et al. (2016) on solitary bees and a study by Jervis et al. (1993) on hymenopteran parasitoids, relatively little is known about the value of farmland forb species to the wider flower-visiting community (*i.e.* non-bee flower-visiting insects). Closing this knowledge gap will improve the efficacy of AES seed mixes, which will be crucial in helping to promote flower-visiting insects and the ecosystem services they provide.

Another problem with current forb-rich margins is the lack of early-flowering species contained in the seed mixes, which means that they are floristically poor during May and early June (Carvell et al., 2007, Holland et al., 2015, Wood et al., 2016). This not only limits their ability to support spring-emerging pollinators (*e.g.* solitary bees and bumblebee queens) (Lye et al., 2009), but also reduces their potential contribution to the pollination of spring-flowering crops, such as oilseed rape (*Brassica napus*) and field bean (*Vicia faba*) (Garratt et al., 2014b, Woodcock et al., 2016a). Clearly, species of spring-flowering plants that occur naturally within field margin habitats which are also attractive to important pollinators of these crops need to be identified and recommended for inclusion within AES seed mixes.

Using 16 predominantly arable farms in central eastern England, a range of pre-existing AES field margin plots were classified as either high or low quality based on their cover and richness of forbs. A suite of ecosystem service, biodiversity and environmental metrics were then quantified within each margin plot and the adjacent crop to address five research objectives: (i) is the quality index a valid and reliable measure of flower-visitor foraging habitat (because margin plots were not experimental treatments, supporting evidence was needed to justify the high/low classification of field margin plots)?; (ii) do AES arable field margins benefit the wider (non-bee) flower-visiting community?; (iii) do high quality field margins promote ecosystem services and biodiversity more effectively than low quality field margins?, and, (iv) does increasing field margin quality promote ecological multifunctionality? This study will provide important information to ecologists and farmers about the additional benefits of creating forb-rich high quality field margins within arable ecosystems. It will also highlight if AES field margin seed mixes need to be optimised to provide better foraging resources for flower-visiting insects.

### 3.2 Data analysis

Detailed descriptions of the study design and survey methods used to achieve the research objectives can be found in Chapter 2. All statistical analyses within this chapter were performed using R v3.2.2 (R Development Core Team, 2016). Where linear and generalised mixed-effect models (LMMs and GLMMs) were applied, the 'lme4' package was used (Bates et al., 2015). All models were validated using Shapiro-Wilk tests and by visual inspection of residual plots to check homogeneity of variance, normally distributed residuals and for model mis-specification (Zuur et al., 2009, Crawley, 2012).

#### 3.2.1. Objective 1: Is the quality index a valid and reliable measure of flower-visitor foraging habitat?

To confirm that the quality index was an accurate reflection of foraging habitat quality, floral resources (number of species in flower and number of floral units), the abundance of flower-visitors and the proportion of flower-visitor feeding observations were compared between margin types using data collected during transect surveys in 2016 (§2.6.2). For this objective, floral resource data and flower-visitor observations were summed across all transect survey rounds. Flower-visitors were grouped into the following taxa for analysis: honeybees, bumblebees, solitary bees, parasitoid wasps, sawflies, day-flying Lepidoptera, hoverflies, non-Syrphid Diptera and beetles. The proportion of feeding observations for each taxa was calculated by dividing the number of observations where the taxa was seen taking pollen/nectar by the total number of observations for that given taxa within each field margin plot. Differences in floral resources, flower-visitor feeding observations and flower-visitor abundance between margin types were investigated using either LMMs or GLMMs, with quality as a fixed effect and site as a random effect. The specific model type, error structure and data transformations for each response variable can be found in Table A3 within the Appendix.

#### 3.2.2. Objective 2: Do AES arable field margins benefit the wider flower-visiting community?

Three approaches were used to achieve this objective. Firstly, field margin floral resources (number of species in flower and number of floral units) were compared between early and late season transect flower surveys to establish the level of floral resource provision within

both periods (§2.6.2). LMMs were used to compare the ln(x) transformed number of floral units between seasons and a GLMM with a negative-binomial error distribution and log-link function was used to compare number of species in flower between seasons. Both models had site as a random effect and transect season (early/late) as a fixed effect. Secondly, using flower-visitation data collected during transect surveys (§2.6.2), the ten most important forage species overall (when considering all flower-visitors) and taxa specific forage preferences were determined. This was done to compare the forage value of species currently included in forb-rich AES seed mixes to those which are not (hereafter referred to as AES and non-AES species, respectively). Whilst there are currently a wide variety of forb-rich AES seed mixes available to farmers (see, for example Anon., 2018, Anon., Undated), they generally include forb species that were trialled in multiple field studies primarily focussed on bumblebees (Carvell et al., 2004, Carvell et al., 2007, Pywell et al., 2011). These 'AES' forb species are listed in Table 3.1 below. Taxa specific flower preferences were examined for bumblebees, honeybees, solitary bees, parasitoid wasps, sawflies, day-flying Lepidoptera, hoverflies, non-Syrphid Diptera and beetles. For each taxon, the percentage of visits to a given flower species were quantified. Then, a forage preference score (FPS) was calculated for that flower species by using the following formula:

$$\mathbf{FPS = (\alpha - \beta)/\beta}$$

Where **α** is the percentage of visits by an insect to a given flower species and **β** is the proportional abundance (%) of that focal flower species (Williams, 2005). Therefore, an FPS of zero indicates no preference, a positive FPS indicates a foraging preference and a negative FPS indicates a non-preference (Williams, 2005). To determine the most important forage species overall, an index was calculated for each flower species based on its interaction frequency and interaction richness. Interaction frequency was calculated by dividing the % of visits a flower species received by its proportional abundance (%) during transect flower surveys (§2.6.2). Similarly, interaction richness was calculated by dividing the percentage of taxa (in relation to all flower-visitor taxa recorded) that visited a given flower species divided by the proportional abundance (%) of the focal flower species during transect surveys. The interaction frequency and interaction richness scores for each flower species were then normalised on a 0-100 scale and averaged to give an importance index score, whereby flower species receiving higher scores were more valuable to flower-visitors. Taxa-specific FPS scores, interaction richness scores, interaction frequency scores and importance index

scores were only calculated for flower species that received >20 visits and that were present within >5 field margin plots.

**Table 3.1.** The forb species included within AES forb-rich field margin seed mixes. These species were included within AES seed mixes after extensive field trials which mainly focussed on bumblebee species (Carvell et al., 2004, Carvell et al., 2007, Pywell et al., 2011).

| | |
|---|---|
| *Achillea millefolium* | *Melilotus officinalis* |
| *Centaurea cyanus* | *Onobrychis viciifolia* |
| *Centaurea nigra* | *Origanum vulgare* |
| *Centaurea scabiosa* | *Phacelia tanacetifolia* |
| *Daucus carota* | *Plantago lanceolata* |
| *Galium verum* | *Plantago media* |
| *Geranium pratense* | *Primula veris* |
| *Knautia arvensis* | *Prunella vulgaris* |
| *Lathyrus pratensis* | *Ranunculus acris* |
| *Leontodon hispidus* | *Rhinanthus minor* |
| *Leucanthemum vulgare* | *Rumex acetosella* |
| *Lotus corniculatus* | *Sanguisorba minor* |
| *Lotus pedunculatus* | *Silene dioica* |
| *Lychnis flos-cuculi* | *Sonchus arvensis* |
| *Malva moschata* | *Trifolium hybridum* |
| *Medicago lupulina* | *Trifolium pratense* |
| *Medicago sativa* | |

### 3.2.3. Objective 3: Do high quality field margins promote ecosystem services and biodiversity more effectively than low quality field margins?

To achieve this objective, a combination of LMMs and GLMMs were used to test the effect of field margin quality on the ecosystem service, invertebrate ecosystem service provider and invertebrate biodiversity response metrics measured during this study. The response metrics examined are listed in Table 3.2 below. For brevity, the specific model type, error structure and data transformations for each response metric can be found in Table A3 in the Appendix. All models included quality as a fixed effect and site as a random effect. However, models for pest control and pollination metrics also included crop position (crop edge/crop

interior) and the interaction between quality and crop position as fixed effects; models for sweep net ecosystem service provider and biodiversity metrics also included sweep net position (margin/crop edge/crop interior) and the interaction between sweep net position and quality as fixed effects; and, models for transect ecosystem service provider and biodiversity metrics also included survey season (early/late) and the interaction between quality and survey season as fixed effects.

**Table 3.2.** The (a) pest control, (b) pollination, (c) soil ecosystem service, (d) invertebrate ecosystem service provider and (e) invertebrate biodiversity metrics compared between high and low quality margin plots. The table also shows how and where each variable was measured.

| Response variables | Survey | Measurement location |
|---|---|---|
| *a) Pest control* | | |
| Calliphora predation index | Field assay | Crop edge and crop interior |
| Ephestia predation index | Field assay | Crop edge and crop interior |
| *b) Pollination* | | |
| No. of fertilised achenes | Field assay | Crop edge and crop interior |
| No. of fruits | Field assay | Crop edge and crop interior |
| *e) Soil ecosystem services* | | |
| Mean soil $K_{fs}$ | Field measurement | |
| Mean soil organic matter content | Soil sample | |
| Mean soil nitrogen content | Soil sample | |
| Mean soil Carbon content | Soil sample | |
| *d) Invertebrate ecosystem service providers* | | |
| Aerial natural enemy abundance | Transects | Margin |
| Aerial crop pest abundance | Transects | Margin |
| Epigeal natural enemy abundance | Pitfall trapping | Margin |
| Epigeal crop pest abundance | Pitfall trapping | Margin |
| Canopy-active natural enemy abundance | Sweep netting | Margin, crop edge and crop interior |
| Canopy-active crop pest abundance | Sweep netting | Margin, crop edge and crop interior |
| *e) Invertebrate biodiversity* | | |
| Lepidoptera abundance | Transects | Margin |
| Lepidoptera richness | Transects | Margin |
| Bumblebee abundance | Transects | Margin |
| Bumblebee richness | Transects | Margin |
| Hoverfly abundance | Transects | Margin |
| Hoverfly richness | Transects | Margin |
| Taxonomic richness | Transects | Margin |
| Taxonomic richness | Pitfall trapping | Margin |
| Taxonomic richness | Sweep netting | Margin, crop edge and crop interior |

### 3.2.4. Objective 4: Does increasing field margin quality promote ecological multifunctionality?

LMMs were used to test if increasing field margin quality promotes ecological multifunctionality, with margin quality entered as a binary fixed effect (low quality = 0, high quality = 1) and site as a random effect. The response variables used to test ecological multifunctionality were the same ecosystem service, ecosystem service provider and biodiversity metrics listed in Table 3.2 above. However, data for metrics measured at different locations (*e.g.* sweep net, pest control and pollination data) or during different seasons (*e.g.* transect data) were pooled. Prior to analysis, each response metrics was standardized on a 0-1 scale using the following formula taken from Herzog et al. (2006):

$$(Yi - Ymin) \div (Ymax - Ymin)$$

Where *Yi* is the observed value, *Ymin* is the minimum observed value and *Ymax* is the maximum observed value for each response metric. This was done to facilitate effect size comparisons between response variables measured using different scales and give a clearer picture of whether increasing field margin quality promotes ecological multifunctionality. Effect sizes were calculated for each response metric by using 95% confidence intervals (CIs) around LMM bootstrap parameter estimates (Dainese et al., 2017). For a given response metric, if CIs did not overlap zero, the effect of field margin quality was significant (*ibid*). Prior to standardisation, several response metrics required transformation to meet LMM assumptions of normality (see Table A3 in the Appendix).

## 3.3 Results

### 3.3.1. Objective 1: Is the quality index a valid and reliable measure of flower-visitor foraging habitat?

A total of 370528 floral units from 112 species of forb and shrub were recorded during transect flower surveys. Both the number of species in flower and number of floral units were significantly greater within high quality margins (floral richness: $\chi^2 = 24.56$, d.f. = 1, $P = <0.001$; number of floral units: $\chi^2 = 62.30$, d.f. = 1, $P = <0.001$) (Figure 3.1). During transect insect surveys 19,033 flower-visitors were observed feeding, which accounted for 62.14% of all insect observations. For eight of nine flower-visiting taxa examined, a significantly greater

proportion of feeding observations were observed within high quality margins (Table 3.3). However, the proportion of sawfly feeding observations did not differ between margin types.

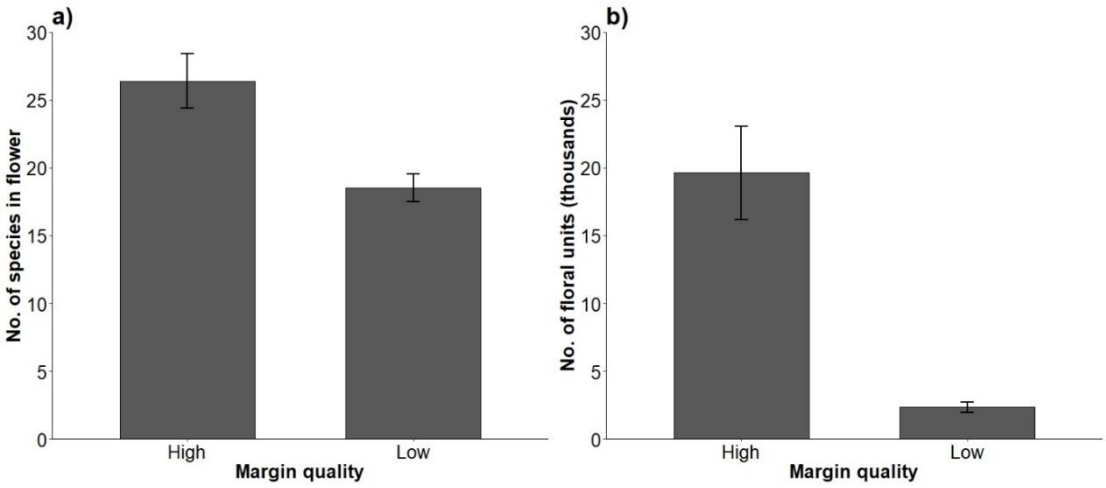


**Figure 3.1.** Mean (± SEM) (a) number of species in flower and (b) number of floral units recorded within high and low quality margin plots during transect surveys.

Analysis of transect data also revealed that all but two flower-visiting taxa were significantly more abundant within high quality margins: whilst mean numbers of sawflies and beetles were greater within high quality margins, the high levels variance recorded for these taxa meant that these differences were not significant (Table 3.4). This probably reflects Interestingly, within high and low quality margins bees and hoverflies constituted only 37.4% and 18.2% of all flower-visiting insects observed during transects, respectively (Figure 3.2). Beetles were the most dominant pollinator taxa in both margin types, but they made up a much higher proportion of the flower visitor community within low quality field margins (high quality margins 28.2%; low quality margins 48.5%) (Figure 3.2). Surprisingly, ≥ 90% of all beetle observations were of Nitidulidae (high quality margins 92.3%; low quality margins 90%). Non-syrphid Diptera were the second most dominant flower-visiting taxa, comprising > 18% of the flower-visitor community recorded within both margin types (high quality margins 18.3%; low quality margins 20.1%). In total, bumblebees and solitary bees (wild bees) were more dominant than managed honeybees (high quality margins: wild bees, 15.3%, honeybees, 11.4%; low quality margins: wild bees, 5.2%, honeybees, 4.5%). However, bumblebees, solitary bees and honeybees constituted a larger proportion of the flower-visitor community within high quality margins (Figure 3.2).

**Table 3.3.** Mean (± SEM) proportion of feeding observations (number of feeding observations divided by the total number of observations) for different flower-visitors recorded within high and low quality field margin plots during transect surveys. Chi-square test statistics and *P*-values are from LMM and GLMM Likelihood Ratio tests (d.f. = 1). Values in bold indicate significant differences between treatments ($P < 0.05$).

| Taxa | High Quality | Low Quality | $X^2$ | *P* |
|---|---|---|---|---|
| Honeybees | 0.98 ± 0.01 | 0.64 ± 0.10 | 38.59 | **<0.001** |
| Bumblebees | 0.69 ± 0.03 | 0.34 ± 0.03 | 50.10 | **<0.001** |
| Solitary bees | 0.70 ± 0.07 | 0.29 ± 0.06 | 13.57 | **<0.001** |
| Parasitoid wasps | 0.55 ± 0.09 | 0.20 ± 0.04 | 14.77 | **<0.001** |
| Sawflies | 0.53 ± 0.08 | 0.49 ± 0.08 | 0.14 | 0.710 |
| Lepidoptera | 0.64 ± 0.03 | 0.11 ± 0.02 | 21.87 | **<0.001** |
| Hoverflies | 0.66 ± 0.05 | 0.30 ± 0.04 | 24.10 | **<0.001** |
| Non-Syrphid Diptera | 0.61 ± 0.07 | 0.29 ± 0.04 | 18.69 | **<0.001** |
| Beetles | 0.95 ± 0.02 | 0.68 ± 0.07 | 7.27 | **0.007** |

**Table 3.4.** Mean (± SEM) abundance of different flower-visitors observed within high and low quality field margin plots during transect surveys. Chi-square test statistics and *P*-values are from LMM and GLMM Likelihood Ratio tests (d.f. = 1). Values in bold indicate significant differences between treatments ($P < 0.05$).

| Taxa | High Quality | Low Quality | $X^2$ | *P* |
|---|---|---|---|---|
| Honeybees | 123.63 ± 45.26 | 15.42 ± 5.64 | 25.33 | **<0.001** |
| Bumblebees | 108.25 ± 9.75 | 18.96 ± 2.23 | 66.26 | **<0.001** |
| Solitary bees | 21.81 ± 3.87 | 6.63 ± 1.72 | 14.44 | **<0.001** |
| Parasitoid wasps | 51.75 ± 8.64 | 16.21 ± 2.96 | 43.16 | **<0.001** |
| Sawflies | 27.75 ± 18.28 | 9.88 ± 2.26 | 1.63 | 0.202 |
| Lepidoptera | 59.25 ± 3.07 | 19.75 ± 2.40 | 40.28 | **<0.001** |
| Hoverflies | 102.63 ± 20.65 | 35.54 ± 4.87 | 21.64 | **<0.001** |
| Non-Syrphid Diptera | 174.25 ± 29.86 | 84.38 ± 7.05 | 11.90 | **<0.001** |
| Beetles | 267.94 ± 83.52 | 204.04 ± 79.99 | 2.09 | 0.149 |

On their own, solitary bees comprised <2.3% of the flower-visitor community (high quality margins 2.2%; low quality margins 1.6%), which was lower than the proportion of Lepidoptera (high quality margins 6.2%; low quality margins 4.7%), parasitoid wasps (high quality margins 5.4%; low quality margins 3.9%) and sawflies (high quality margins 2.9%; low quality margins 2.3%) (Figure 3.2). More than 75% of all sawfly observations within both margin types were of Cephidae (high quality margins 84.2%; low quality margins 78.5%).

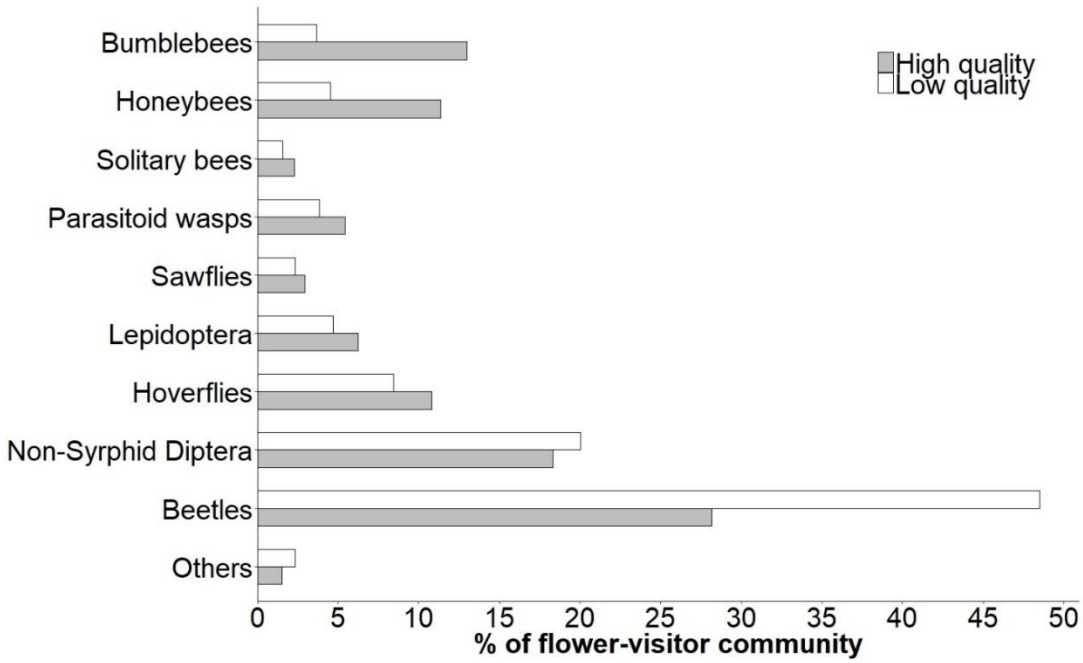


**Figure 3.2.** The flower-visiting insect community observed within field margin plots during transect surveys.

### 3.3.2. Objective 2: Do AES arable field margins benefit the wider flower-visiting community?

The number of species in flower and number of floral units present within field margin plots were significantly lower during early season transect surveys (number of species in flower: $\chi^2 = 70.49$, d.f. = 1, P = <0.001; number of floral units: $\chi^2 = 21.85$, d.f. = 1, P = <0.001) (Figure 3.3). Flower-visiting insects overwhelmingly visited forbs (visits = 98.59%), with only a small proportion of visits observed on shrubs and grasses (shrub visits = 0.75%, grass visits = 0.67%). Strikingly, when considering all flower-visitors, only two of the ten most important forage plants were AES species (*Sonchus arvensis* and *Daucus carota*) (Figure 3.4). Taxa-specific forage preferences also revealed that non-AES species were more attractive than AES species for all groups except honeybees, where AES species accounted for two of the three most popular forage plants (*Malva moschata* and *C. nigra*) (Table 3.5).

For all other taxa, AES species accounted for none (bumblebees and sawflies) or one (solitary bees, parasitoid wasps, day-flying Lepidoptera, hoverflies, non-Syrphid Diptera and beetles) of the three most popular forage plants (Table 3.5). Large flower preference scores were recorded for parasitoid wasps (FPS = 81.08) and beetles (FPS = 45.57) on *Heracleum sphondylium*, and for sawflies (FPS = 104.92) on *Taraxacum* spp. (Table 3.5). In terms of plant

families, parasitoid wasps, hoverflies and non-Syrphid Diptera preferred Apiaceae species, honeybees and beetles preferred Asteraceae species, whilst solitary bees preferred Ranunculaceae species. Bumblebees and sawflies displayed no family preference (Table 3.5).

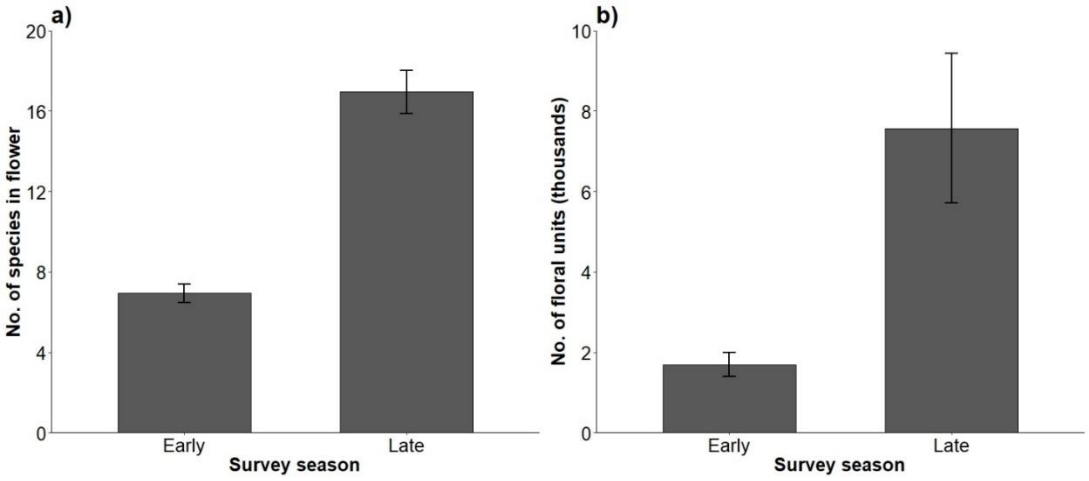


**Figure 3.3.** Mean (± SEM) (a) number of species in flower and (b) number of floral units recorded within field margin plots during early and late transect survey seasons.

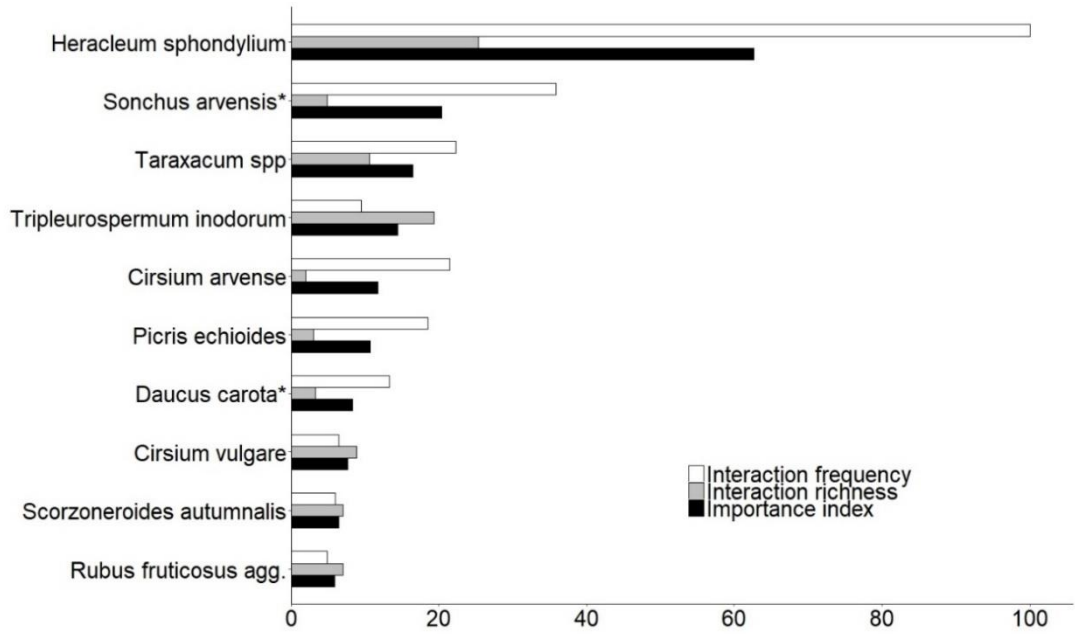


**Figure 3.4.** Showing the normalised (0-100) interaction frequency, normalised (0-100) interaction richness and importance index for the ten most important flower-visiting insect forage plants within field margins during transect surveys. Flower species with an asterisk are those sown as part of forb-rich AES seed mixes. Only plants species with >20 observations and present within >5 margins were considered.

**Table 3.5.** Flower preference scores (FPS) for the three most popular forage plants visited by individual flower-visitor taxa during transect surveys. Species with an asterisk are those sown as part of forb-rich AES seed mixes. Only plants species with >20 observations and present within >5 margins were considered.

| **Honeybees** | **FPS** | **Bumblebees** | **FPS** | **Solitary bees** | **FPS** |
|---|---|---|---|---|---|
| *Malva moschata** | 3.39 | *Stachys sylvatica* | 7.3 | *Ranunculus acris** | 2.69 |
| *Centaurea nigra** | 2.47 | *Cirsium vulgare* | 4.98 | *Ranunculus repens* | 1.81 |
| *Cirsium arvense* | 1.67 | *Rubus fruticosus* agg. | 3.23 | *Anthriscus sylvestris* | 1.75 |
| **Parasitoid wasps** | **FPS** | **Sawflies** | **FPS** | **Lepidoptera** | **FPS** |
| *Heracleum sphondylium* | 81.08 | *Taraxacum* spp | 104.92 | *Rubus fruticosus* agg. | 6.15 |
| *Daucus carota** | 19.1 | *Ranunculus repens* | 5.04 | *Knautia arvensis** | 5.99 |
| *Anthriscus sylvestris* | 3.93 | *Anthriscus sylvestris* | 1.49 | *Cirsium arvense* | 1.95 |
| **Hoverflies** | **FPS** | **Non-Syrphid Diptera** | **FPS** | **Beetles** | **FPS** |
| *Daucus carota** | 9.28 | *Heracleum sphondylium* | 21.63 | *Heracleum sphondylium* | 45.57 |
| *Picris echioides* | 5.63 | *Daucus carota** | 12.23 | *Cirsium arvense* | 10.39 |
| *Heracleum sphondylium* | 5.46 | *Tripleurospermum inodorum* | 11.29 | *Sonchus arvensis** | 19.03 |

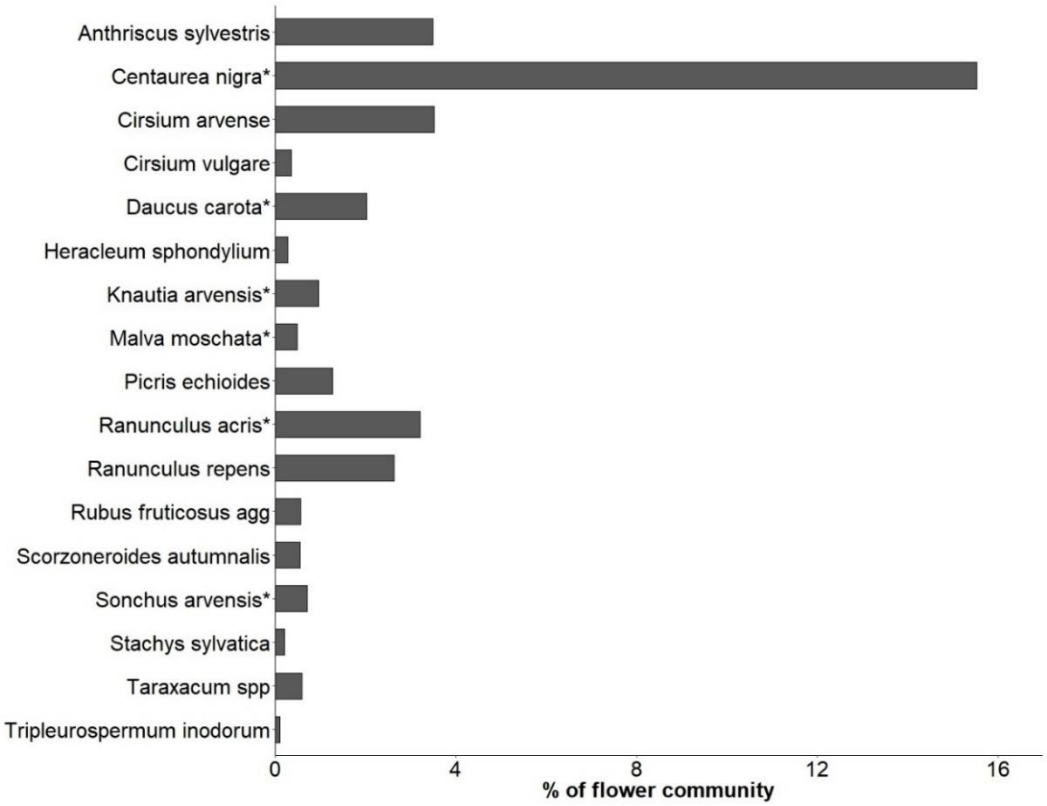


**Figure 3.5.** The relative abundance (% number of floral units) for important forage plants recorded during transect flower surveys in 2016. Species with an asterisk are those sown as part of forb-rich AES seed mixes.

Overall, 68.9% of all floral units recorded within field margins belonged to AES species. The non-AES species listed in Figure 3.4 and Table 3.5 that were important for flower-visitors accounted between 0.1% (*Tripleurospermum inodorum*) and 3.5% (*Anthriscus sylvestris* and *Cirsium arvense*) of the field margin flower community (Figure 3.5).

### 3.3.3. Objective 3: Do high quality field margins promote ecosystem services and biodiversity more effectively than low quality field margins?

*3.3.3.1. Effect of field margin quality on ecosystem service provision*

Margin quality had a highly significant effect on all four pollination and pest control metrics (Table 3.6; Figure 3.6), as they were recorded at greater levels adjacent to high quality margins. Pest control metrics were also significantly affected by crop position (Table 3.6; Figure 3.6), with higher levels of pest control were recorded at the crop edge than within the crop interior. In contrast, crop position had no effect on strawberry pollination (Table 3.6; Figure 3.6).

**Table 3.6.** Results from LMMs and GLMMs (Chi-square likelihood ratio tests, d.f. and *p*-values) analysing: the effect of margin quality and crop position on (a) pest control and (b) pollination services; and (c), the effect of margin quality on soil ecosystem services. Significant results ($P$ <0.05) are presented in bold.

| | Quality | | | Crop position | | | Quality x Crop position | | |
|---|---|---|---|---|---|---|---|---|---|
| | $\chi^2$ | d.f. | *P* | $\chi^2$ | d.f. | *P* | $\chi^2$ | d.f. | *P* |
| *a) Pest control metrics* | | | | | | | | | |
| *Calliphora* predn index | 25.85 | 1 | **<0.001** | 7.23 | 1 | **0.027** | 0.93 | 3 | 0.336 |
| *Ephestia* predn index | 32.26 | 1 | **<0.001** | 10.51 | 1 | **0.005** | 4.67 | 3 | **0.031** |
| *b) Pollination metrics* | | | | | | | | | |
| No. of fertilised achenes | 25.10 | 1 | **<0.001** | 1.96 | 1 | 0.376 | 0.41 | 3 | 0.523 |
| No. of strawberry fruits | 12.21 | 1 | **0.002** | 0.43 | 1 | 0.805 | 0.03 | 3 | 0.867 |
| *c) Soil services* | | | | | | | | | |
| Soil $K_{fs}$ | 35.64 | 1 | **<0.001** | | | | | | |
| Soil organic matter | 3.74 | 1 | 0.053 | | | | | | |
| Soil nitrogen | 1.13 | 1 | 0.288 | | | | | | |
| Soil carbon | 0.26 | 1 | 0.613 | | | | | | |

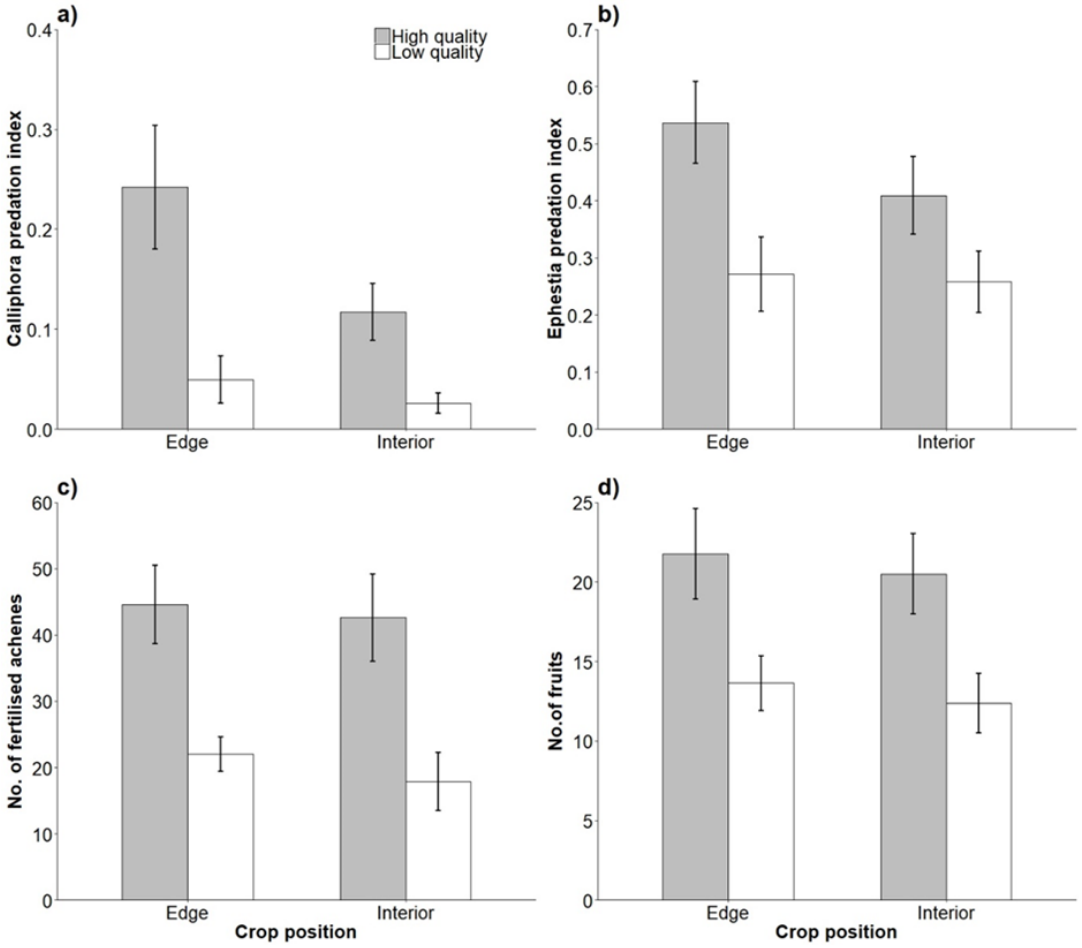


**Figure 3.6.** Mean (± SEM) *Calliphora* and *Ephestia* predation index (a, b), number of fertilised achenes (c), and number of strawberry fruits (d) recorded adjacent to high and low quality margin plots at the crop edge and crop interior (20 metres into the crop).

The interaction between margin quality and crop position was only significant for *Ephestia* predation (Table 3.6; Figure 3.6); since, *Ephestia* predation was greater adjacent to high quality margins at both the crop edge and interior, but the level of *Ephestia* predation adjacent to low quality margins remained similar at both the crop edge and interior. The effect of margin quality on soil organic matter %, soil nitrogen and soil carbon was non-significant, with all three metrics being relatively even between margin types (Table 3.6; Figure 3.7). Conversely, margin quality had a highly significant effect on soil $K_{fs}$ ($\chi^2$ = 35.64, d.f. = 1, $P$ = <0.001), as $K_{fs}$ was much greater within high quality margins plots (Table 3.6; Figure 3.7).

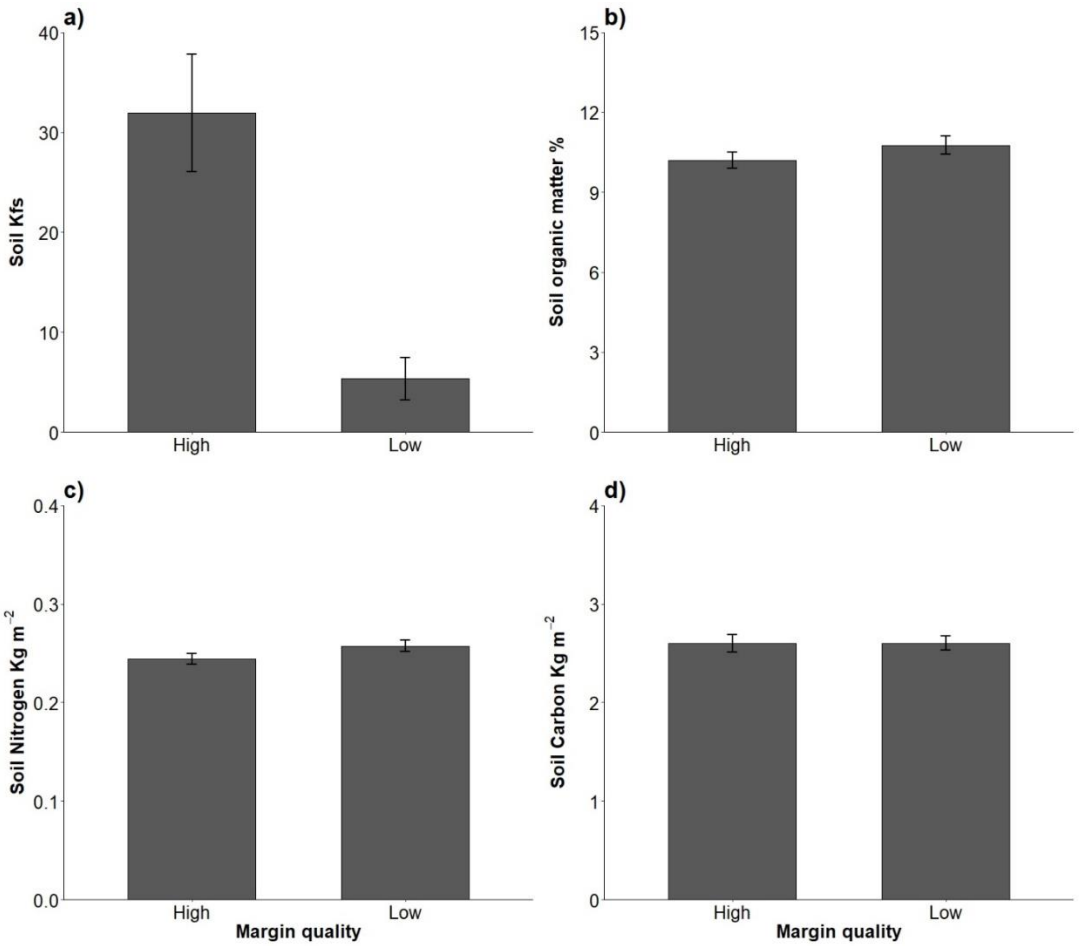


**Figure 3.7.** Mean (± SEM) (a) soil $K_{fs}$, (b) soil organic matter %, (c) soil nitrogen Kg $m^{-2}$ and (d) soil carbon Kg $m^{-2}$ recorded within high and low quality margin plots.

*3.3.3.2. Effect of field margin quality on invertebrate ecosystem service providers*

A total of 10843 crop pollinators were recorded during transect surveys. During transects, pitfall trapping and sweep netting at total of 39128 natural enemies and 23908 crop pests were recorded. Both margin quality and survey season had a significant effect on the abundance of crop pollinators, and aerial natural enemies and crop pests (Table 3.7a). The abundance of these ecosystem service provider groups was greater within high quality margins and during late season transect surveys (Figure 3.8a, b, c). The interaction between margin quality and survey season also had a significant effect of the abundance of crop pollinators and natural enemies during transect surveys (Table 3.7a), with the differences in abundance between margins types being much greater during late season transect surveys (Figure 3.8a, b). Crop pest abundance during transects was unaffected by the interaction of quality and survey season (Table 3.7a; Figure 3.8c).

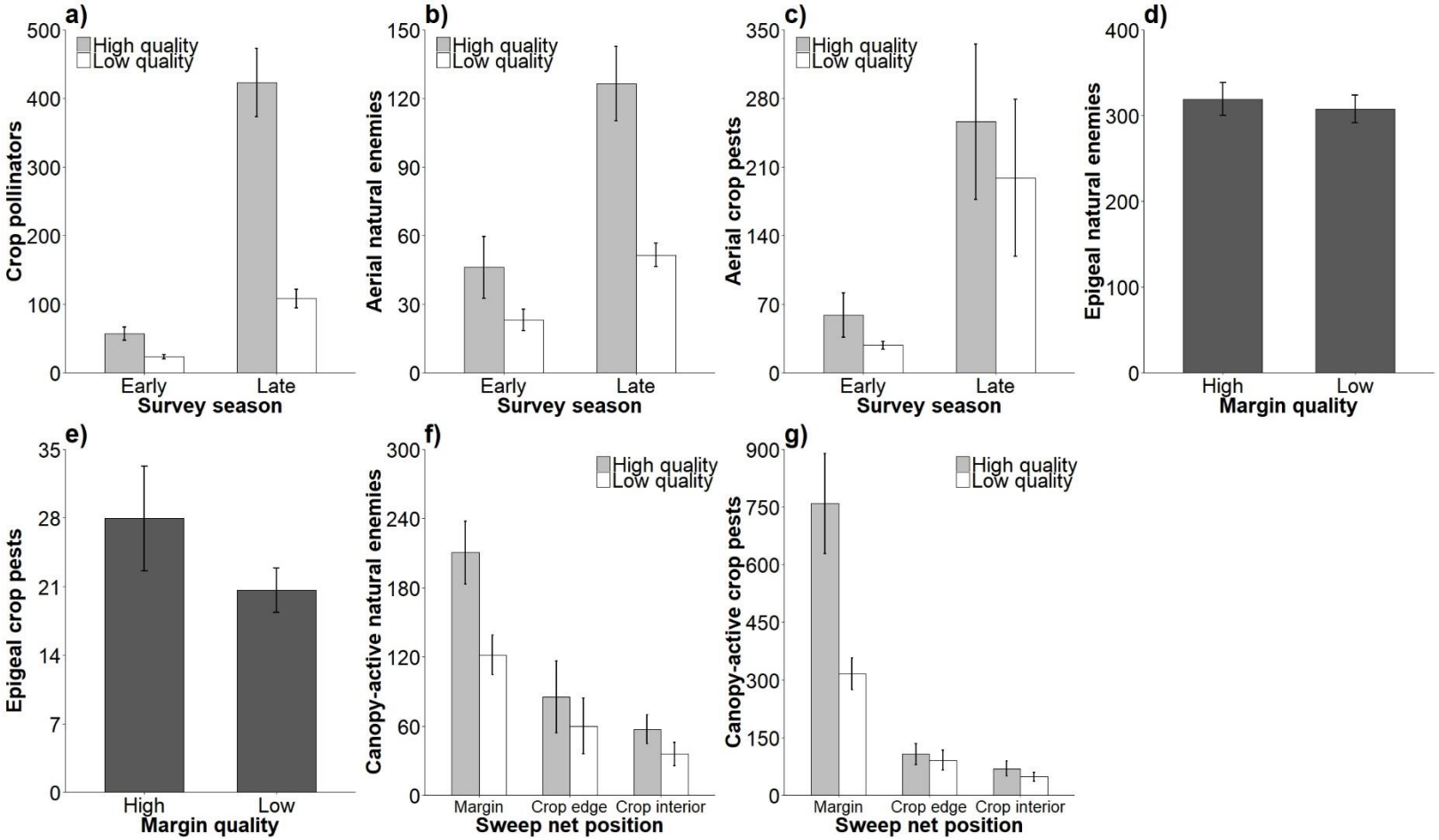


**Figure 3.8.** Mean (± SEM) abundance of (a) crop pollinators, (b) aerial natural enemies and (c) crop pests recorded within high and low quality margin plots during early and late transect survey seasons; mean (± SEM) abundance of (d) epigeal natural enemies and (e) crop pests recorded within high and low-quality margin plots during pitfall trapping; mean (± SEM) abundance of (f) canopy-active natural enemies and (g) crop pest recorded within high and low quality margin plots, the crop edge and crop interior during sweep-net surveys.

**Table 3.7.** Results from LMMs and GLMMs (Chi-square likelihood ratio tests, d.f. and p-values) analysing: (a) the effect of margin quality and survey season on invertebrate ecosystem service providers recorded within field margin plots during transects; (b) the effect of margin quality on invertebrate ecosystem service providers recorded within field margin plots during pitfall trapping; and (c), the effect of margin quality and sample position on invertebrate ecosystem service providers recorded during sweep netting. Significant results ($P$ <0.05) are presented in bold.

| | **Quality** | | | **Season** | | | **Quality x Season** | | |
|---|---|---|---|---|---|---|---|---|---|
| | $\chi^2$ | d.f. | *P* | $\chi^2$ | d.f. | *P* | $\chi^2$ | d.f. | *P* |
| *a) Transects* | | | | | | | | | |
| Crop pollinators | 42.88 | 1 | **<0.001** | 96.76 | 1 | **<0.001** | 4.3 | 3 | **0.038** |
| Aerial natural enemies | 32.1 | 1 | **<0.001** | 46.18 | 1 | **<0.001** | 5.93 | 3 | **0.015** |
| Aerial crop pests | 6.53 | 1 | **0.038** | 21.35 | 1 | **<0.001** | 2.26 | 3 | 0.133 |

| | **Quality** | | |
|---|---|---|---|
| | $\chi^2$ | d.f. | *P* |
| *b) Pitfall trapping* | | | |
| Epigeal natural enemies | 0.64 | 1 | 0.425 |
| Epigeal crop pests | 1.18 | 1 | 0.277 |

| | **Quality** | | | **Sweep net position** | | | **Quality x sweep net position** | | |
|---|---|---|---|---|---|---|---|---|---|
| | $\chi^2$ | d.f. | *P* | $\chi^2$ | d.f. | *P* | $\chi^2$ | d.f. | *P* |
| *c) Sweep netting* | | | | | | | | | |
| Canopy-active natural enemies | 15.66 | 1 | **0.001** | 52.37 | 2 | **<0.001** | 0.59 | 5 | 0.746 |
| Canopy-active crop pests | 14.9 | 1 | **0.002** | 74.73 | 2 | **<0.001** | 6.48 | 5 | **0.039** |

During pitfall trapping margin quality had no effect on the abundance of epigeal natural enemies or crop pests (Table 3.7b; Figure 3.8d, e). Conversely, margin quality had a significant effect on canopy-active natural enemies and crop pests (Table 3.7c), with both groups being recorded in greater numbers within and adjacent to high quality field margins (Figure 3.8f, g). Sweep net position also had a highly significant effect on the abundance of canopy-active natural enemies and crop pests (Table 3.7c), as numbers of both groups monotonically decreased from the margin to the crop interior (Figure 3.8f, g). The interaction between quality and sweep net position only had a significant effect on the abundance of canopy-active crop pests (Table 3.7c), as differences in abundance between margin types during margin sweep net surveys were much greater than at either the crop edge or crop interior (Figure 3.8f, g).

*3.3.3.3. Effect of field margin quality on invertebrate biodiversity*

In total, 1422 day-flying Lepidoptera of 26 species, 2187 bumblebees of eight species and 2495 hoverflies of 33 species were observed during transect surveys. *Maniola jurtina* (223 individuals), *Bombus lapidarius* (694) and *Melanostoma* spp. (757) were the most abundant day-flying Lepidoptera, bumblebee and hoverfly species, respectively. Nitidulidae were the most abundant taxa during transect surveys and sweep netting (Transects 7942, sweep netting 3956), and Collembola were the dominant taxa during pitfall trapping (16152). Both margin quality and survey season had a highly significant effect (*P* <0.001) on the abundance and richness of Lepidoptera, bumblebees and hoverflies during transects (Table 3.8a), with all metrics being recorded at greater levels within high quality margins and during late season surveys (Figure 3.9).

**Table 3.8.** Results from LMMs (Chi-square likelihood ratio tests, d.f. and *p*-values) analysing: (a) the effect of margin quality and survey season on invertebrate biodiversity metrics measured within field margin plots during transects; (b) the effect of margin quality on taxonomic richness during pitfall trapping; and (c), the effect of margin quality and sample position on taxonomic richness during sweep netting. Significant results (*P* <0.05) are presented in bold.

| | Quality | | | Season | | | Quality x Season | | |
|---|---|---|---|---|---|---|---|---|---|
| | $\chi^2$ | d.f. | *P* | $\chi^2$ | d.f. | *P* | $\chi^2$ | d.f. | *P* |
| *a) Transects* | | | | | | | | | |
| Lepidoptera abundance | 29.32 | 1 | **<0.001** | 103.88 | 1 | **<0.001** | 5.28 | 3 | **0.022** |
| Lepidoptera richness | 27.51 | 1 | **<0.001** | 106.84 | 1 | **<0.001** | 5.16 | 3 | **0.023** |
| Bumblebee abundance | 74.76 | 1 | **<0.001** | 124.99 | 1 | **<0.001** | 8.59 | 3 | **0.003** |
| Bumblebee richness | 26.27 | 1 | **<0.001** | 77.75 | 1 | **<0.001** | 3.44 | 3 | 0.064 |
| Hoverfly abundance | 28.64 | 1 | **<0.001** | 73.39 | 1 | **<0.001** | 7.96 | 3 | **0.005** |
| Hoverfly richness | 14.03 | 1 | **<0.001** | 57.54 | 1 | **<0.001** | 4.09 | 3 | **0.043** |
| Taxonomic richness | 7.31 | 1 | **0.026** | 32.48 | 1 | **<0.001** | 1.5 | 3 | 0.221 |

| | Quality | | |
|---|---|---|---|
| | $\chi^2$ | d.f. | *P* |
| *b) Pitfall trapping* | | | |
| Taxonomic richness | 0.34 | 1 | 0.56 |

| | Quality | | | Sweep net position | | | Quality x Sweep net position | | |
|---|---|---|---|---|---|---|---|---|---|
| | $\chi^2$ | d.f. | *P* | $\chi^2$ | d.f. | *P* | $\chi^2$ | d.f. | *P* |
| *c) Sweep netting* | | | | | | | | | |
| Taxonomic richness | 39.89 | 1 | **<0.001** | 93.64 | 2 | **<0.001** | 6.76 | 5 | **0.034** |

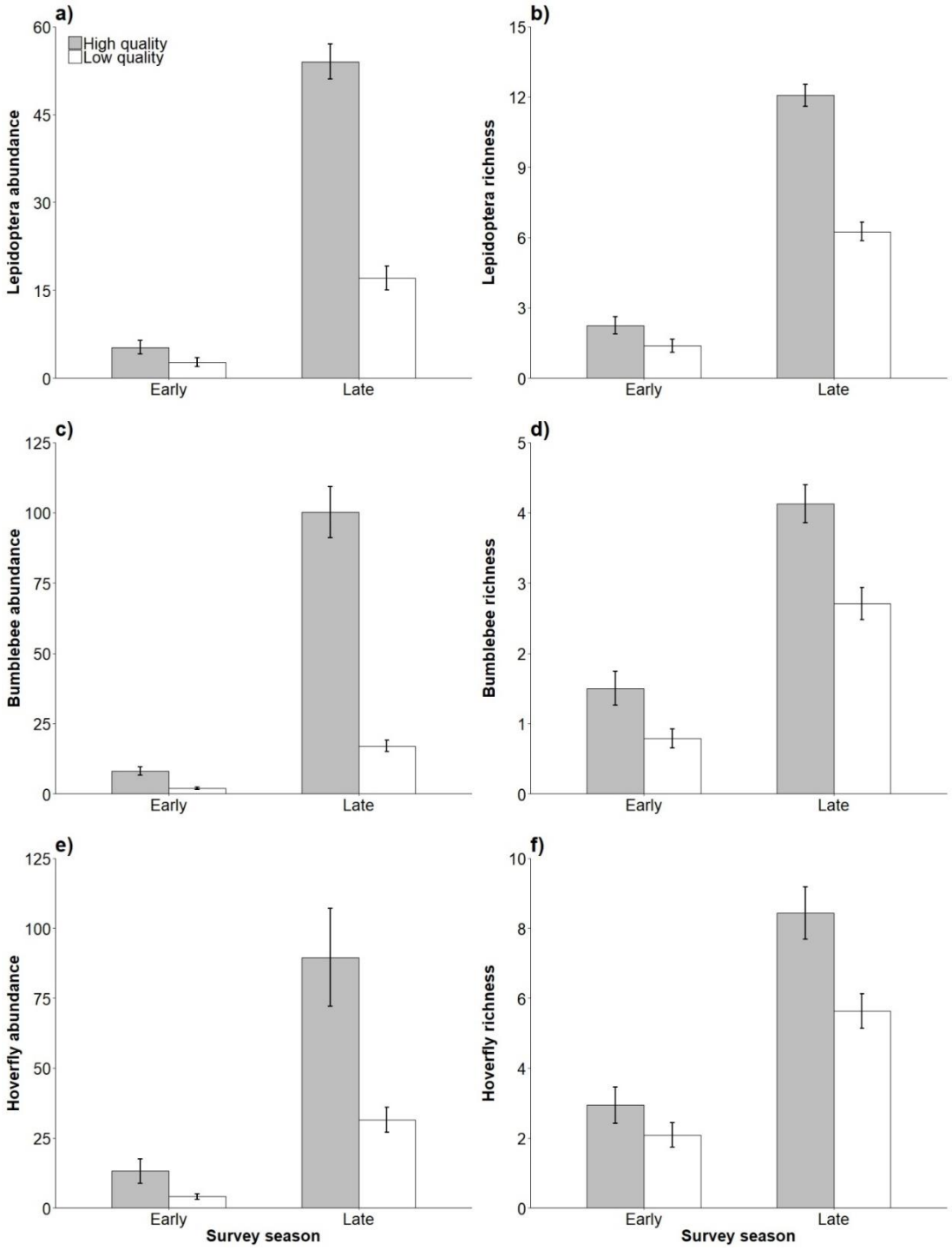


**Figure 3.9.** Mean (± SEM) (a) Lepidoptera abundance, (b) Lepidoptera richness, (c) bumblebee abundance, (d) bumblebee richness, (c) hoverfly abundance and (d) hoverfly richness recorded within high and low quality margin plots during early and late season transect surveys.

The interaction between margin quality and survey season also had a significant effect on butterfly abundance and richness (Table 3.8a), bumblebee abundance, and hoverfly abundance and richness, as the differences in abundance between margins types were much greater during late season transect surveys (Figure 3.9). The interaction between quality and season had a marginally significant effect on bumblebee richness (Table 3.8a; Figure 3.9d).

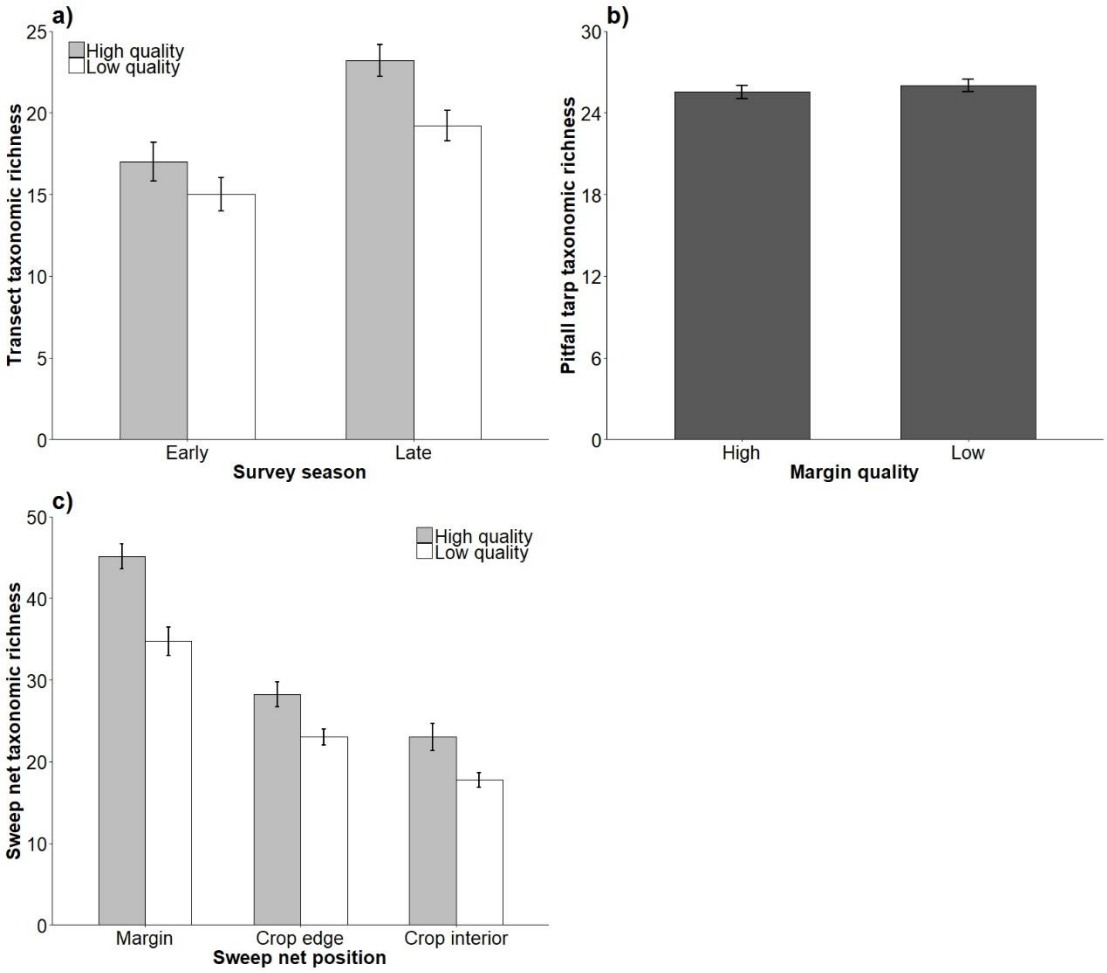


**Figure 3.10.** Mean (± SEM): (a) taxonomic richness recorded within high and low quality margin plots during early and late season transect surveys; (b) taxonomic richness recorded within high and low quality margin plots during pitfall trapping; (c) taxonomic richness recorded within high and low quality margin plots, the crop edge and crop interior during sweep net surveys.

Margin quality and season also had a significant effect on invertebrate taxonomic richness during transect surveys (Table 3.8a), since taxonomic richness was greater within high quality

margins and during late season transect surveys (Figure 3.10a). Furthermore, the interaction between quality and survey season had significant effect on invertebrate taxonomic richness during transects (Table 3.8a), as the differences between margin types were greater during late season transect surveys (Figure 3.10a).

During pitfall trapping, margin quality had no effect on invertebrate taxonomic richness (Table 3.8b; Figure 3.10b), but during sweep netting it had a significant effect (Table 3.8c), with greater taxonomic richness being recorded within high quality margins (Figure 3.10c). Sweep net taxonomic richness was also significantly affected by position and the interaction between quality and position (Table 3.8c), as it monotonically decreased from the margin to the crop interior and the effect of quality was greater during margin sweep net surveys (Figure 3.10).

*3.3.3.4. Effect of field margin quality on transect floral resources*

The number of species in flower and number of floral units recorded during transect flower surveys followed a similar pattern to invertebrate ecosystem service providers and biodiversity, being significantly greater within high quality margins and during late season surveys (Table 3.9; Figure 3.11). The interaction between quality and survey season also had a significant effect on both the number of species in flower and the number of floral units (Table 3.9), since for both metrics the effect of margin quality was much greater during the late season (Figure 3.11).

**Table 3.9.** Results from LMMs (Chi-square likelihood ratio tests, d.f. and *p*-values) analysing the effect of margin quality and survey season on the number of species in flower and the number of floral units recorded within field margin plots during transect surveys. Significant results ($P$ <0.05) are presented in bold.

| | Quality | | | Season | | | Quality x Season | | |
|---|---|---|---|---|---|---|---|---|---|
| | $\chi^2$ | d.f. | *P* | $\chi^2$ | d.f. | *P* | $\chi^2$ | d.f. | *P* |
| No. species in flower | 27.62 | 1 | **<0.001** | 87.34 | 1 | **<0.001** | 5.28 | 3 | **0.022** |
| No. of floral units | 50.86 | 1 | **<0.001** | 39.85 | 1 | **<0.001** | 6.76 | 3 | **0.009** |

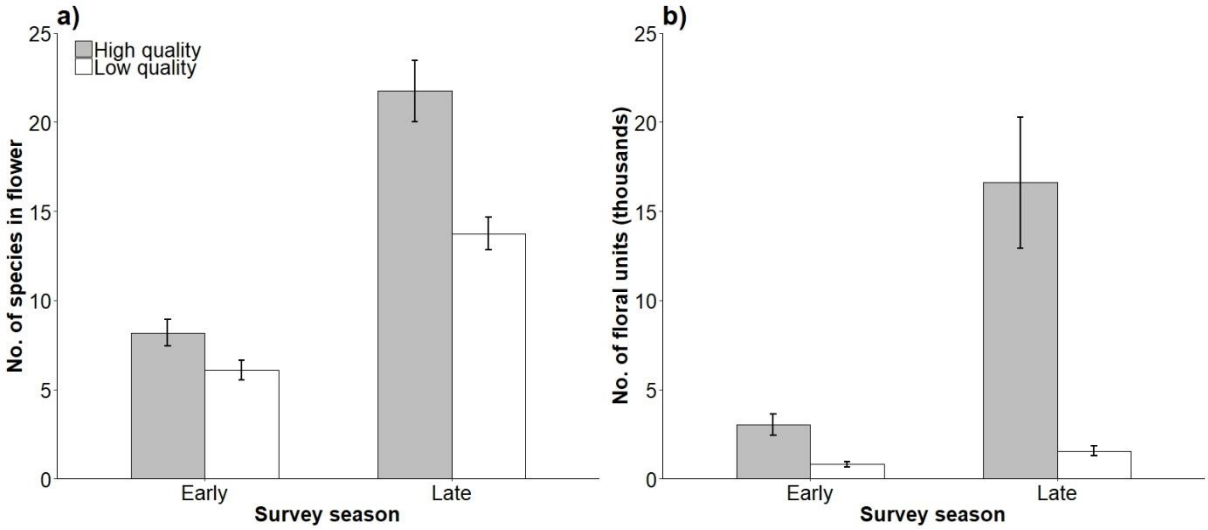


**Figure 3.11.** Mean (± SEM) (a) number of species in flower and (b) number of floral units (thousands) recorded within high and low quality margin plots during early and late transect survey seasons.

**Objective 4: Does increasing field margin quality promote ecological multifunctionality?**

Overall, increasing field margin quality had a significant positive effect on 17 out of the 24 ecosystem service and biodiversity metrics tested (Figure 3.12), which suggests high quality forb-rich field margins promote ecological multifunctionality. In general, margin quality had a greater effect on invertebrate mediated ecosystem services (pest control and pollination) and biodiversity than on soil services. Indeed, increasing margin quality had a strong and significant effect on all four pollination and pest control metrics. Conversely, increasing margin quality had a small negative effect on soil organic matter, soil nitrogen and soil carbon, but this effect was not significant (Figure 3.12a). However, increasing margin quality had a significant positive effect on soil $K_{fs}$ (Figure 3.12a). When just considering ecosystem service providers, increasing margin quality had a positive effect on every metric, but this was only significant for transect crop pollinators and natural enemies, and sweep net natural enemies and crop pests (Figure 3.12b). For biodiversity metrics, increasing margin quality had a significant positive effect for all variables except pitfall trap taxonomic richness, where the effect was negative but non-significant (Figure 3.12c). The strongest positive response to increasing margin quality was bumblebee abundance during transects (Figure 3.12c).

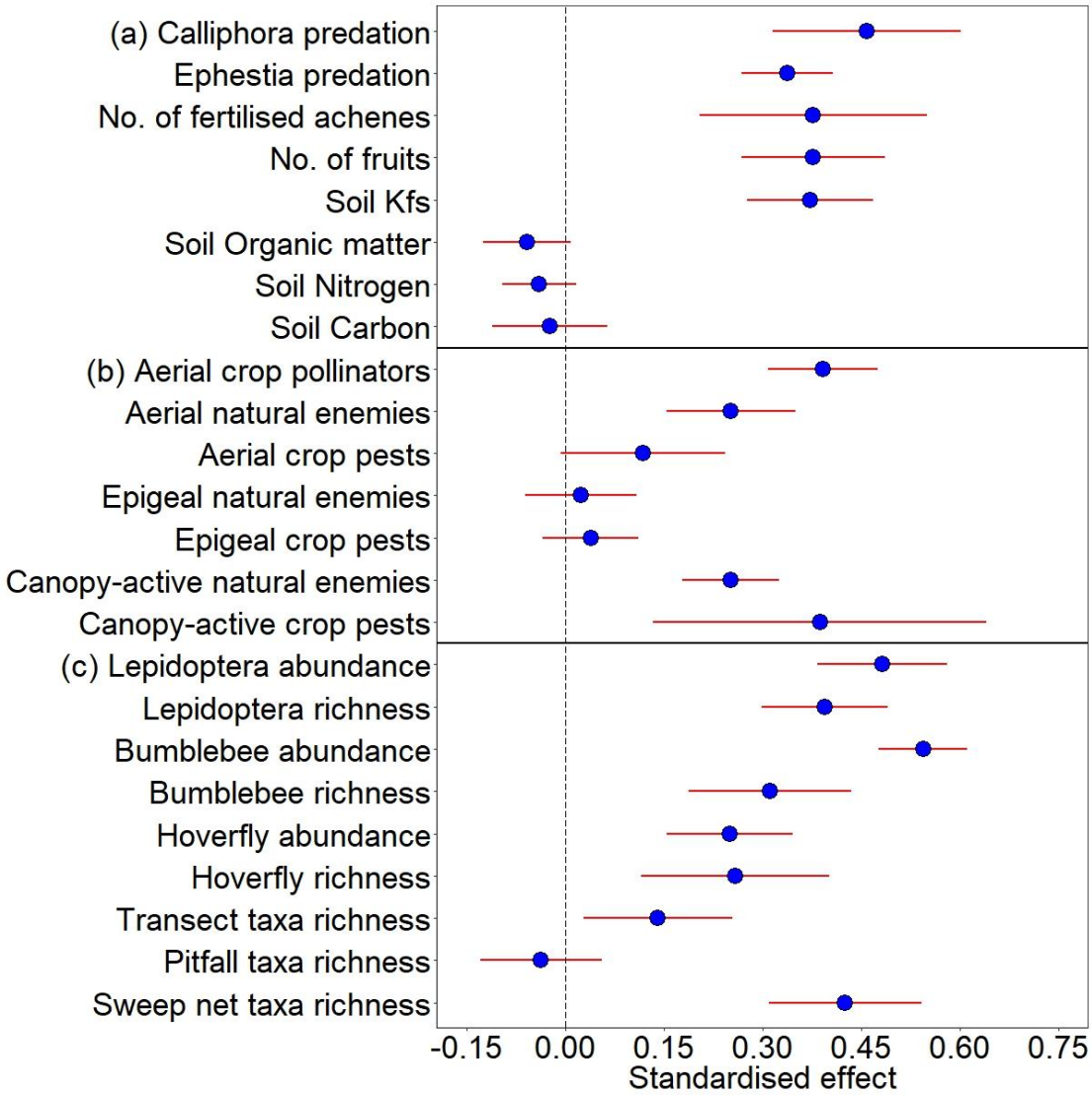


**Figure 3.12.** Standardised effect of field margin quality on (a) ecosystem service, (b) invertebrate ecosystem service provider and (c) invertebrate biodiversity metrics measured during this study. Dots represent the bootstrap parameter estimate for each metric and lines represent 95% confidence intervals; where they do not cross zero, the effect of field margin quality is significant ($P$ <0.05).

### 3.4 Discussion

This is the first study to investigate whether high quality forb-rich field margins can enhance multiple ecosystem services simultaneously alongside their objective of supporting farmland pollinators. The results suggest that, compared to low quality field margins, high quality margins demonstrated greater biological control, pollination, soil infiltration and biodiversity potential. In the subsequent sections findings will be discussed within the context of the original research objectives.

### 3.4.1. Objective 1: Is the quality index a valid and reliable measure of flower-visitor foraging habitat?

Compared to low quality margins, high quality margins provided more floral resources, better pollinator foraging habitat and supported greater numbers of most flower-visitor taxa examined. This confirmed that the high/low classification accurately reflected a margins value as flower-visitor foraging habitat. Until recently, most studies on the biodiversity benefits of forb-rich field margins have focussed on wild bees and hoverflies (Carvell et al., 2007, Haenke et al., 2009, Scheper et al., 2013, Scheper et al., 2015). Consequently, we have limited knowledge about how the wider flower-visiting community responds pollinator friendly management (but see Grass et al., 2016).

One interesting finding that emerged from this study is that field margins support a much wider range of flower-visiting taxa than bees and hoverflies, including beetles, non-Syrphid Diptera, day-flying Lepidoptera, parasitoid wasps and sawflies. In fact, these groups were much more abundant than bees and hoverflies, which mirrors the findings of Grass et al. (2016) who found that 75% of the flower-visiting species recorded within wildflower plantings were either hoverflies or bees. This highlights the need for future assessments of field margin conservation and ecosystem service value to consider the wider flower-visiting community, especially given that species within these less popular groups provide important ecosystem services such as crop pollination (*e.g.* non-Syrphid Diptera) (Orford et al., 2015, Rader et al., 2016), biological control (e.g. beetles and non-Syrphid Diptera) (Holland et al., 2008) and cultural value (*e.g.* day-flying Lepidoptera) (King et al., 2017).

### 3.4.2. Do AES arable field margins benefit the wider flower-visiting community?

Comparisons of seasonal floral richness and abundance highlighted that AES field margins are floristically poor during May and early June compared to July and August, which is a pattern that has been recorded elsewhere (Carvell et al., 2007, Holland et al., 2015). This is probably because AES seed mixes tend not include early flowering species such as *Anthriscus sylvestris, Ranunculus repens* and *Taraxacum* agg. (Carvell et al., 2004, Carvell et al., 2007, Pywell et al., 2011). Including these early flowering species in AES seed mixes would be especially beneficial to spring emerging pollinators such as solitary bees and bumblebee queens (Carreck and Williams, 2002, Wood et al., 2016). It would also increase the density of pollinating insects within and around fields at a time when mass-flowering crops such as oilseed rape are in bloom, which should have positive effects on yield (Jauker et al., 2012). Indeed, Campbell et

al. (2017b) found that *Taraxacum* agg. abundance within orchards was positively related to apple (*Malus domestica*) flower visitation by wild insects and suggested that including this species within orchard flower strips would enhance both early-season pollinators and apple pollination.

The inclusion of additional species to improve AES seed mixes for flower-visitors was further supported by flower-visitation data, since eight of the ten most important forage plants overall were non-AES species, and when considering individual flower-visiting taxa, at least one AES-species occurred in the top three forage plants for each group investigated. Of particular interest was that non-AES species were important for parasitoid wasps and hoverflies. Both groups play an important role in controlling crop pests and flower-visitation data suggests that their populations could potentially be enhanced by encouraging plant species such as *A. sylvestris* (parasitoid wasps), *H. sphondylium* (parasitoid wasps and hoverflies) and *Picris echioides* (hoverflies). Given that AES flower mixes were designed based on the foraging preferences of bumblebees, it is somewhat surprising that they displayed (along with sawflies) the strongest preference for non-AES species, including *Stachys sylvatica, Cirsium vulgare* and *Rubus fruticosus* agg. Table 3.10 below lists the non-AES species that were found to be the most valuable to flower-visiting insects. Despite their importance as forage plants, they only accounted for a small proportion of the floral units recorded during transect flower surveys. It is likely that the addition of these species to seed mixes would increase the efficacy of current AES options by providing resources for a more diverse variety of flower-visitors. This may help to reverse the biotic homogenisation of pollinator communities that has taken place across the UK (Carvalheiro et al., 2013), which will, in turn, make agro-ecosystems more resilient to environmental change (Winfree and Kremen, 2009, Senapathi et al., 2015).

However, several of the important forage plants listed in Table 3.10 are either hedgerow plants (e.g. *A. sylvestris*, *H. sphondylium*, *Rubus fruticosus* agg, *S. sylvatica*) or arable weeds (e.g. *Tripleurospermum inodorum*) (Rose et al., 2006). As such, they may be better enhanced using existing AES options that promote sympathetic management of the crop (*e.g.* unharvested cereal headlands) and hedgerows (*e.g.* reduce cutting of hedges and verges) (Natural England, 2013b, a). Moreover, species such as *Cirsium arvense, C. vulgare, H. sphondylium* and *Taraxacum* spp are unlikely to be encouraged by famers because of their potentially detrimental agronomic impact. For example, *C. arvense* and *C. vulgare* are listed as pernicious weeds in the UK, therefore landowners are required to limit their spread into adjacent areas (Mortimer et al., 2006). Also, *H. sphondylium* is a potential host and source of

carrot fly (*Psila rosae*) (Degen et al., 1999a, b, c), and in this study, beetles and sawflies displayed an overwhelming preference for *H. sphondylium* and *Taraxacum* agg., respectively. But both taxa were dominated by families which contain agronomically important pest species: Nitidulidae represented >90% of flower-visiting beetle observations and Cephidae represented >90% of sawfly observations (AHDB, 2014). It is unclear whether encouraging these flower species would also enhance populations of Nitidulidae and Cephidae within agro-ecosystems and lead to increases in crop damage. Such trade-offs need to be explored before populations of these species are encouraged within arable systems.

**Table 3.10.** The most valuable non-AES species for flower-visiting insects during transect surveys.

| |
|---|
| *Anthriscus sylvestris* |
| *Cirsium arvense* |
| *Cirsium vulgare* |
| *Heracleum sphondylium* |
| *Picris echioides* |
| *Ranunculus repens* |
| *Rubus fruticosus* agg |
| *Scorzoneroides autumnalis* |
| *Stachys sylvatica* |
| *Taraxacum* spp |
| *Tripleurospermum inodorum* |

### 3.4.3. Objective 3: do high quality field margins promote ecosystem services and biodiversity more effectively than low quality field margins?

*3.4.3.1. The effect of quality on ecosystem service provision*

Because forb-rich margins generally support greater numbers of flower-visiting insects than forb-poor margins, it is hypothesised that they will enhance pollination within the adjacent crop (Wratten et al., 2012, Korpela et al., 2013). Several recent studies support this hypothesis (Blaauw and Isaacs, 2014a, Feltham et al., 2015, Pywell et al., 2015), as do the findings of this study, since strawberry phytometers adjacent to high quality margins produced a greater number of fertilised achenes and fruits. Likewise, since many natural enemies of crop pests consume pollen and nectar (Wäckers et al., 2005), and these resources can increase their longevity, fecundity and activity (Wäckers, 1994, Tylianakis et al., 2004, Witting-Bissinger et al., 2008, van Rijn et al., 2013), forb-rich margins should also enhance pest control in the

adjacent crop via increases in local and within-field populations of natural enemies (Gurr et al., 2017). Blaauw and Isaacs (2015) found this to be the case, as pest control and natural enemy abundance within the crop canopy were greater within commercial blueberry fields adjacent to forb-rich margins than in fields adjacent to grass margins. In the present study, significantly greater levels of *Calliphora* and *Ephestia* predation were recorded within fields adjacent to high quality margin plots. These findings add to the growing body of evidence which suggests that forb-rich field margins can be used as a tool to enhance agricultural production by mediating elevated levels of crop pollination and pest control (Blaauw and Isaacs, 2014a, 2015, Pywell et al., 2015, Woodcock et al., 2016a, Sutter et al., 2017a).

Most soil services were unaffected by margin quality, but soil infiltration rate was significantly greater within high quality margins. This is probably because compared to low quality margins, high quality plots had significantly greater plant species richness and legume cover, as well as significantly less cover of grasses (see Table 2.2 in §2.2), and plant species richness can indirectly enhance soil infiltration via increases in soil porosity and soil organic carbon (Fischer et al., 2015). Furthermore, soil infiltration rate is also greater in the presence of legumes than in the presence of either grasses or non-leguminous forbs due to increases in soil porosity mediated by differences in root structure and elevated Lumbricidae populations (Mytton et al., 1993, Mitchell et al., 1995, Obi, 1999, Fischer et al., 2014, Gould et al., 2016, Huang et al., 2017). This finding highlights the flood alleviation potential of forb-rich field margins.

Both plant species richness and legumes can also have a positive effect on soil carbon, nitrogen and organic matter within semi-natural grassland biotopes (Fornara and Tilman, 2008, De Deyn et al., 2011, Cong et al., 2014). It is therefore surprising that quality had no effect on these variables in this study. One possible explanation for this is that the mensurative approach used introduced confounding variables which made it difficult to detect the effect of margin quality. Potential confounding variables include field margin age and fertiliser drift. Soil carbon, nitrogen and organic matter accumulate over time (Knops and Tilman, 2000, McLauchlan et al., 2006), and granular nitrogen fertiliser can drift up to 4 m into the adjacent field margin during spinning disc application within the crop (Tsiouris and Marshall, 1998). Fertiliser drift would not only lead to increases in soil nitrogen (Jenkinson et al., 2004), but also greater soil carbon and organic matter content due to increases in primary productivity and litter inputs (Jones and Donnelly, 2004, Dijkstra et al., 2005). The field margin plots used here were at least two years old, but their approximate age could not be verified.

Furthermore, it is reasonable to assume that field margin plots received varying levels of fertiliser inputs via drift since this factor was not controlled for.

*3.4.3.2. The effect of quality on invertebrate ecosystem system service providers and biodiversity*

The abundance of crop pollinators, aerial natural enemies, canopy-active natural enemies, and the abundance and richness of bumblebees, day-flying Lepidoptera and hoverflies were all significantly greater within high quality margins. This is unsurprising given that the quality index used to classify each margin was based on the cover and richness of forbs, and pollen and nectar is the primary food source for these insect groups (Nicolson, 2007). Nonetheless, these results add to the large body of research which demonstrates the importance of forb-rich biotopes to farmland flower-visitors (Haaland et al., 2011, Scheper et al., 2013, Scheper et al., 2015, Wood et al., 2015c). This study adds to a small but growing body of research examining the effect of forb-rich field margins on the wider invertebrate community (Thomas and Marshall, 1999, Clarke et al., 2007, Pywell et al., 2011, Holland et al., 2013). In line with previous research (*ibid*), the results here suggest that forb-rich field margins support a more diverse invertebrate community than forb-poor grass margins, as significantly more invertebrate taxa were recorded within high quality field margins during transects and sweep net surveys. This demonstrates that increasing the richness and abundance of forbs within arable field margins could conserve a wider array of invertebrate taxa than just flower-visiting insects. However, during pitfall trapping, the richness of invertebrate taxa, and the abundance of epigeal natural enemies and crop pests did not differ between margin types. This mirrors the findings of Meek et al. (2002), who found no differences in the abundance and richness of epigeal invertebrate groups caught by pitfall trapping between forb-rich and forb-poor field margins.

The findings of Grass et al. (2016) suggested that forb-rich margins enhance the abundance of pollen beetles (*Meligethes aeneus*) in the late flowering season and Eggenschwiler et al. (2013) found that forb-rich field margins had +191 % higher slug activity density than grass margins. Few other studies have explored whether forb-rich margins enhance the abundance of agronomically important crop pests. Worryingly, this study found that, compared to low quality forb-poor margins, forb-rich high quality margins supported significantly greater numbers of aerial and canopy-active crop pests. In some ways this finding is unsurprising given that many crop pests (*e.g.* pollen beetles and certain Lepidoptera) are

known flower-visitors (Willmer, 2011, Orford et al., 2016). Furthermore, by supporting a greater richness and abundance of forbs, high quality margins provide a wider range of host plant resources for phytophagous crop pests and may thereby enhance their local populations (Moreira et al., 2016).

Perhaps even more concerning is that the greater number of crop pests recorded in high quality margins did not translate into reduced pest populations. This contradicts the pest control assay results recorded here, as well as the general consensus of previous work which suggests that, in general, greater levels of pest control are achieved when local natural enemy populations become larger (Blaauw and Isaacs, 2012, Blaauw and Isaacs, 2015, Woodcock et al., 2016a, Dainese et al., 2017, Gurr et al., 2017). Yet, factors other than natural enemy abundance can exert a strong influence on crop pest populations, e.g., the plants found in arable field margins in this study may have been more attractive to crop pests than natural enemies and/or the greater numbers of natural enemies recorded within high quality margins may have led to increases in intraguild predation (see Tscharntke et al., 2016, and references therein). Evidently, more work is required to determine the mechanisms that simultaneously promote elevated crop pest and natural enemy numbers within forb-rich field margins and to establish whether this translates into greater levels of crop damage.

*3.4.3.3. Spill-over and seasonal differences in ecosystem service provision and biodiversity*

During transects, all invertebrate biodiversity and ecosystem service provider metrics were recorded at significantly greater levels during late season surveys. Field margin floral abundance and richness was also significantly greater during late season transect surveys, which suggests that seasonal differences in invertebrate biodiversity and ecosystem service providers were being driven by changes in foraging resources. Moreover, for all but two invertebrate groups measured (bumblebee richness and the abundance of aerial crop pests), there was a significant interaction between margin quality and season, which indicated that the differences between margin types were much greater during late season transect surveys. Again, this mirrored the seasonal patterns of floral resources, which further supports the above suggestion that the efficacy of forb-rich margins can be increased during the early season by sowing a wider array of spring flowering forb species.

Regardless of margin type, *Calliphora* and *Ephestia* predation, canopy-active natural enemies and crop pests, and the number of invertebrate taxa recorded during sweep net surveys significantly decreased further into the crop, which is a pattern that has been recorded

elsewhere (Tschumi et al., 2016b, Woodcock et al., 2016a). On the other hand, there was no difference in the delivery of pollination services between the crop edge and crop interior. Furthermore, compared to low quality margins, greater levels of pest control and pollination, and numbers of invertebrate taxa were recorded within the crop interior adjacent to high quality margins. In line with several previous studies, this suggests that forb-rich field margins enhance the spill-over of these services into the adjacent crop (Blaauw and Isaacs, 2014a, 2015, Tschumi et al., 2016a, Woodcock et al., 2016a), which further highlights their agronomic and ecological benefits.

### 3.4.4. Objective 4: does increasing field margin quality promote ecological multifunctionality?

By increasing the local richness and abundance of forb species, and removing land from cultivation, high quality field margins should not only benefit flower-visiting insects, but also a range of ecosystem services that are important to agricultural production and wider society (Wratten et al., 2012, Holland et al., 2017b, Isbell et al., 2017). It has been established that high quality forb-rich field margins enhance the local abundance and richness of flower-visitors, and the pest control and pollination services delivered to the adjacent crop. But few studies have assessed these benefits in combination, and no studies have explored the additional ecosystem services that forb-rich field margins may provide. When examining the effect of margin quality in isolation on invertebrate biodiversity and ecosystem service provision, this study found that increasing the richness and abundance of forbs enhances the delivery of multiple ecosystem services, including pest control, pollination and soil infiltration capacity. Increasing margin quality also enhanced the abundance of crop pollinators and natural enemies (aerial and canopy-active), the abundance and richness of bumblebees, day-flying Lepidoptera and hoverflies, and the richness of invertebrate taxa. In total, increasing field margin quality increased 17 out of the 24 ecosystem service and biodiversity metrics tested. This study clearly demonstrates that forb-rich margins enhance ecosystem multifunctionality, which suggests that farmers could receive additional AES payments for these supplementary services (Reed et al., 2014, Smith and Sullivan, 2014). Along with the agronomic benefits of forb-rich field margins, additional AES payments may increase the uptake of forb-rich field margin options (Wratten et al., 2012, Bommarco et al., 2013). If so, this would be a positive step towards adopting the principles of ecological intensification within modern agro-ecosystems. However, the enhancement of canopy-active crop pests by

forb-rich field margins may reduce the willingness of farmers to adopt such schemes. We must therefore establish the agronomic implications of this finding and seek ways in which it can be mitigated.

### 3.5 Conclusion

This study highlights the multiple benefits that high quality forb-rich field margins can deliver to agriculture and wider-society. When compared to low quality control margins, high quality margins supported greater numbers of important ecosystem service providers, and greater levels of invertebrate biodiversity, pollination, pest control and soil infiltration. However, there was some evidence that high quality margins also supported greater numbers of crop pests. Furthermore, whilst the effect of margin quality on soil carbon, nitrogen and organic matter was contrary to previous findings (De Deyn et al., 2011, Cong et al., 2014), it is likely that this result was due to statistical noise added to the data set by confounding variables. Finally, in line with recent studies (Holland et al., 2015, Wood et al., 2015b, Wood et al., 2016), the efficacy of AES flower margins would be greatly improved by increasing the diversity of plant species included in the seed mixes. Early flowering species would be particularly beneficial, however additional research needs to establish if target species enhance populations of flower-visiting crop pests before they are included.

# Chapter 4: Does landscape composition influence invertebrate biodiversity and ecosystem service provision within arable field margins?

### 4.1 Introduction

Post-war agricultural intensification has significantly altered land-use patterns within Europe and North America (Wilcove et al., 1998, Donald et al., 2001, Tilman et al., 2001, Robinson and Sutherland, 2002, Benton et al., 2003, Donald et al., 2006, van Vliet et al., 2015). Specifically, by converting large areas of semi-natural habitat to farmland and removing field boundary elements, intensive agriculture has degraded landscapes to such an extent that only small patches of uncropped land remain (Robinson and Sutherland, 2002, Tscharntke et al., 2002, Benton et al., 2003, Haines-Young et al., 2003). For example, in England and Wales approximately 50% of the hedgerow stock was removed between 1940 and 2000 (Robinson and Sutherland, 2002), and it is thought that up to 97% of forb-rich grasslands within the United Kingdom have been lost since the 1930s (NCC, 1984, Howard et al., 2003). Losses on this scale are worrisome because uncropped land provides farmland invertebrates with shelter from farm operations and a suite of crucial habitat resources (*e.g.* overwintering sites, food and breeding habitat) (Landis et al., 2000, Pywell et al., 2005a, Carvell et al., 2007, Isaacs et al., 2009, Merckx et al., 2010, Roulston and Goodell, 2011). Indeed, there is accumulating evidence that these losses are driving the long-term declines in farmland invertebrates and degrading the ecosystem services they provide (Donald, 1998, Tscharntke et al., 2005, Bianchi et al., 2006, Biesmeijer et al., 2006, Winfree et al., 2009, Chaplin-Kramer et al., 2011, Kennedy et al., 2013, Potts et al., 2016). At the same time, rising agrochemical inputs and disturbance regimes have effectively excluded many invertebrate taxa from the crop (Dover, 1996, 1997, Stoate et al., 2001, Duelli and Obrist, 2003, Geiger et al., 2010, Ewald et al., 2015, Woodcock et al., 2016b, Marko et al., 2017). And so, any remaining uncropped areas act as important source habitats from which invertebrates colonise the crop to deliver vital services, such as pollination and natural pest control (Bianchi et al., 2006, Ockinger and Smith, 2007, Blaauw and Isaacs, 2014a, 2015, Woodcock et al., 2016a, Cole et al., 2017).

Several authors have hypothesised that increasing the relative proportion of uncropped land within agro-ecosystems would help to sustain and restore farmland invertebrate populations and the ecosystem services they provide (Kremen et al., 2004, Tscharntke et al., 2005, Bianchi et al., 2006, Kremen et al., 2007). In response, manifold studies have explored the relationships between the area of uncropped land, farmland invertebrate biodiversity and ecosystem service provision (see, for example Steffan-Dewenter, 2002, 2003, Chaplin-Kramer et al., 2011, Thies et al., 2011, Shackelford et al., 2013). In general, research findings support this hypothesis (Chaplin-Kramer et al., 2011, Thies et al., 2011, Kennedy et al., 2013, Rusch et al., 2013a, Shackelford et al., 2013, Veres et al., 2013, Martins et al., 2015,

Nicholson et al., 2017). For example, Chaplin-Kramer et al. (2011) conducted a meta-analysis of 46 studies and found a positive relationship between the amount of uncropped land in the surrounding landscape and natural enemy diversity and abundance, and the predation and parasitism of crop pests. Similarly, in a global study of 39 different crop systems, Kennedy et al. (2013) found that both wild bee richness and abundance were greater within agricultural landscapes comprising more uncropped land. Furthermore, both insect visitation rates and yields are enhanced in a range of agronomically important crops with increasing proportions of uncropped land in the surrounding landscape (Holzschuh et al., 2012, Klein et al., 2012, Martins et al., 2015).

Despite strong evidence supporting positive relationships between uncropped land, invertebrate biodiversity and invertebrate mediated ecosystem services, variability between studies is high and there is evidence that, in some cases, increasing proportions of uncropped land has a benign or negative effect (Westphal et al., 2003, Winfree et al., 2008, Schuepp et al., 2011, Winqvist et al., 2011, Tscharntke et al., 2016). These contradictory results could be because, for certain invertebrate taxa and ecosystem services, other biotopes are more important (Westphal et al., 2003, Carre et al., 2009, Tscharntke et al., 2016, Senapathi et al., 2017). For example, some generalist invertebrate species are adapted to highly disturbed agricultural biotopes (*e.g.* arable land and intensive grassland), which provide them with more abundant food resources than those that are found within uncropped land (Westrich, 1996, Holland et al., 2004, Holland et al., 2005, Holland et al., 2009, Blitzer et al., 2012, Schellhorn et al., 2015, Woodcock et al., 2016b). Several recent studies have also highlighted the potential importance of urban biotopes for insect pollinators (Cane et al., 2006, Winfree et al., 2007, Carre et al., 2009, Baldock et al., 2015, Sirohi et al., 2015). Baldock et al. (2015) and Sirohi et al. (2015) found that urban biotopes contain greater species richness of bees than either farmland or nature reserves, respectively. Agricultural and urban biotopes are clearly important to specific invertebrate taxa, but their impact on farmland invertebrate populations and ecosystem service provision remains largely unexplored (but see, (Westphal et al., 2003, Winfree et al., 2007, Carre et al., 2009, Fuentes-Montemayor et al., 2011, Winqvist et al., 2011).

Management prescriptions attempting to maximise one ecosystem service can often reduce the provision of other services (*i.e.* a trade-off: +/-) (Bennett et al., 2009, Nelson et al., 2009, Power, 2010) or, in some cases, enhance multiple services simultaneously (*i.e.* synergy: +/+) (Shackelford et al., 2013, Dainese et al., 2017, Sutter et al., 2017a). To effectively manage agro-ecosystems for multiple ecosystem services, we need to know whether a given

management prescription for one service will lead to trade-offs and/or synergies with other services (Shackelford et al., 2013). For example, increasing the proportion of uncropped land may be beneficial to wild bees (Kennedy et al., 2013), but could be detrimental to carabid beetles (Winqvist et al., 2011). Taxa-specific information would allow farmers to make informed decisions about which taxa they would like to prioritise (*e.g.* a farmer who grows a large proportion of pollinator-dependant crops is likely to prioritise wild bees over carabids). However, there is a paucity of information on the trade-offs and synergies promoted by increasing the amount of uncropped land within agro-ecosystems because studies have tended to focus on either a single ecosystem service (*e.g.* pollination), a single ecosystem service provider (*e.g.* insect pollinators) or a single invertebrate taxon (*e.g.* wild bees) (but see Shackelford et al., 2013, Holland et al., 2015, Sutter et al., 2017a).

This chapter aims to further disentangle the effects of landscape composition on farmland invertebrate populations and the ecosystem services they provide. Invertebrate biodiversity and invertebrate mediated ecosystem services were measured within a range of pre-existing field margin plots distributed across 16 arable farms in central eastern England. The proportion of uncropped land, arable land, agricultural grassland and urban areas were then quantified within 1 km, 500 m and 250 m radii surrounding each margin plot. This data was used to explore relationships between the proportions of different biotopes in the surrounding landscape and: (i) the delivery of pest control and pollination services; (ii) the abundance of invertebrate ecosystem service and disservice providers; and, (iii) the amount of invertebrate biodiversity. To the authors knowledge, this is the first study to simultaneously investigate how the relative proportion of different biotopes at multiple spatial scales affects invertebrate biodiversity, invertebrate ecosystem service/disservice providers and invertebrate mediated ecosystem services.

**4.2 Data Analysis**

Study design and data collection methods are outlined in Chapter 2. All statistical analyses within this chapter were performed using R v3.2.2 (R Development Core Team, 2016). Linear and generalised linear models (LMs and GLMs, respectively) were used to test the effect of landscape composition on: (i) pest control and pollination service provision; (ii) the abundance of crop pollinators, natural enemies and crop pests; and, (iii) the amount invertebrate biodiversity recorded within and adjacent to arable field margins (Table 4.1). For each of these response variables, margin quality was not included as fixed effect within GLMs or LMs

because the specific focus of this chapter was to examine the influence of landscape composition. All models were validated by visually inspecting residual plots and applying Shapiro-Wilk tests to check the distribution of residuals, homogeneity of variance and model mis-specification (Zuur et al., 2009, Crawley, 2012). Table A4 in the Appendix describes the LMs, GLMs, error structures and transformations used to test the relationship between landscape composition metrics and the response variables explored within this chapter. Soil ecosystem services were omitted from landscape composition analysis because they are unlikely to be affected by the proportion of different biotopes within the surrounding landscape.

**Table 4.1.** (a) Pest control, (b) pollination, (c) invertebrate ecosystem service provider and (e) invertebrate biodiversity response variables used during landscape composition analysis. The table also shows how and where each variable was measured.

| Response variables | Survey | Measurement location |
|---|---|---|
| *a) Pest control* | | |
| Calliphora predation index | Field assay | Crop edge and crop interior |
| Ephestia predation index | Field assay | Crop edge and crop interior |
| *b) Pollination* | | |
| No. of fertilised achenes | Field assay | Crop edge and crop interior |
| No. of fruits | Field assay | Crop edge and crop interior |
| *c) Invertebrate ecosystem service providers* | | |
| Aerial natural enemy abundance | Transects | Margin |
| Aerial crop pest abundance | Transects | Margin |
| Epigeal natural enemy abundance | Pitfall trapping | Margin |
| Epigeal crop pest abundance | Pitfall trapping | Margin |
| Canopy-active natural enemy abundance | Sweep netting | Margin, crop edge and crop interior |
| Canopy-active crop pest abundance | Sweep netting | Margin, crop edge and crop interior |
| *d) Invertebrate biodiversity* | | |
| Lepidoptera abundance | Transects | Margin |
| Lepidoptera richness | Transects | Margin |
| Bumblebee abundance | Transects | Margin |
| Bumblebee richness | Transects | Margin |
| Hoverfly abundance | Transects | Margin |
| Hoverfly richness | Transects | Margin |
| Taxonomic richness | Transects | Margin |
| Taxonomic richness | Pitfall trapping | Margin |
| Taxonomic richness | Sweep netting | Margin, crop edge and crop interior |

The effect of landscape composition was assessed within 1 km, 500 m and 250 m radii surrounding each margin plot using four discrete biotope classes: (i) arable (all areas where crops were grown); (ii) agricultural grassland (all grassland that was grazed and/or cut for silage); (iii) urban (farm buildings, private houses, roads and gardens); and, (iv) uncropped land (rough grassland, field margins, hedgerows, woodlands, scrub, ditches, ponds and rivers). Crop position (pollination and pest control metrics), transect survey season (transect ecosystem service provider and biodiversity metrics) and sweep net survey position (sweep net ecosystem service provider and biodiversity metrics), as well as their interactions with landscape composition metrics, were also included as fixed effects within initial models (but only if they passed the $R^2$ and collinearity selection process described below). However, only significant interactions are discussed, since the main effects of transect survey season and sweep net survey position were explored in detail within Chapter 3.

Owing to the large number of predictors, variables were only included within initial models if they had $R^2$ values >0.05. Collinearity between predictors was then checked using Pearson correlation tests (see Table A5 in Appendix for correlation matrices of landscape composition metrics). Where selected variables had correlation coefficients >0.65 or variance inflation factors >3, the variables with the lowest $R^2$ values were removed from the initial model (Zuur et al., 2009, Zuur et al., 2010). Models were simplified using a backward-stepwise deletion procedure from the starting model until only significant predictors ($P$ <0.05) remained (Zuur et al., 2009, Crawley, 2012). At each deletion step, models were assessed using either an $F$ test (LMs) or a Chi-square test (GLMs) for a significant increase in residual deviance. If the removal of a non-significant landscape metric significantly increased the residual deviance, it was re-entered into the model (Zuur et al., 2009, Crawley, 2012).

**4.3 Results**

In total, landscape composition influenced eleven out of the 19 invertebrate biodiversity and ecosystem service variables tested. There was considerable variation in the cover of biotope classes during each survey and at each spatial scale between study farms (Table 4.2). However, there were some general patterns across surveys. For example, sample landscapes were dominated by arable biotopes, with agricultural grassland and uncropped land being the next most dominant biotopes, and urban land being the least dominant biotope (Table 4.2).

### 4.3.1. Pest control and pollination

Overall, landscape composition exerted a strong influence on pest control and pollination services (Table 4.3). Pest control variables were affected by landscape composition metrics at 1 km, whereas pollination variables were equally affected by landscape composition metrics at 1 km and 250 m (Table 4.3). *Calliphora* predation increased as the proportion of agricultural grassland at 1 km increased (Table 4.3a; Figure 4.1a).

**Table 4.2.** Mean (± SEM), minimum and maximum percent cover of different biotope classes measured within 1 km, 500 m and 250 m radii surrounding margin plots used during (a) transects, (b) pitfall trapping or (c) sweep netting/field assays.

| Biotope class | Area (%) | Minimum (%) | Maximum (%) |
|---|---|---|---|
| *a) Transects* | | | |
| Arable land % 1 km | 62.38 ± 2.29 | 33.76 | 88.56 |
| Arable land % 500 m | 69.14 ± 2.54 | 30.97 | 89.93 |
| Arable land % 250 m | 73.81 ± 2.57 | 30.52 | 94.41 |
| Agricultural grassland % 1 km | 17.32 ± 2.26 | 1.95 | 53.61 |
| Agricultural grassland % 500 m | 13.05 ± 2.31 | 0.00 | 60.01 |
| Agricultural grassland % 250 m | 10.35 ± 2.30 | 0.00 | 60.07 |
| Urban land % 1 km | 4.80 ± 0.48 | 0.68 | 10.64 |
| Urban land % 500 m | 2.89 ± 0.78 | 0.00 | 29.01 |
| Urban land % 250 m | 1.55 ± 0.56 | 0.00 | 19.23 |
| Uncropped land % 1 km | 15.53 ± 0.68 | 8.73 | 30.44 |
| Uncropped land % 500 m | 14.92 ± 0.84 | 8.13 | 40.34 |
| Uncropped land % 250 m | 14.29 ± 1.08 | 5.59 | 38.14 |
| *b) Pitfall trapping* | | | |
| Arable land % 1 km | 62.59 ± 1.49 | 33.76 | 90.76 |
| Arable land % 500 m | 68.46 ± 1.69 | 20.19 | 93.97 |
| Arable land % 250 m | 73.98 ± 1.62 | 25.16 | 96.49 |
| Agricultural grassland % 1 km | 17.12 ± 1.49 | 0.00 | 53.61 |
| Agricultural grassland % 500 m | 12.83 ± 1.48 | 0.00 | 60.01 |
| Agricultural grassland % 250 m | 8.67 ± 1.37 | 0.00 | 60.07 |
| Urban land % 1 km | 4.64 ± 0.36 | 0.35 | 22.21 |
| Urban land % 500 m | 3.11 ± 0.47 | 0.00 | 29.01 |
| Urban land % 250 m | 1.69 ± 0.34 | 0.00 | 19.92 |
| Uncropped land % 1 km | 15.67 ± 0.55 | 8.66 | 35.43 |
| Uncropped land % 500 m | 15.96 ± 0.73 | 6.03 | 43.86 |
| Uncropped land % 250 m | 15.65 ± 0.91 | 3.51 | 51.30 |
| *c) Sweep netting/field assays* | | | |
| Arable land % 1 km | 67.17 ± 2.86 | 44.88 | 79.27 |
| Arable land % 500 m | 70.67 ± 3.15 | 42.69 | 86.55 |
| Arable land % 250 m | 72.14 ± 4.07 | 47.12 | 94.41 |
| Agricultural grassland % 1 km | 12.30 ± 2.09 | 2.86 | 28.95 |
| Agricultural grassland % 500 m | 10.56 ± 1.90 | 0.00 | 23.66 |
| Agricultural grassland % 250 m | 11.66 ± 2.91 | 0.00 | 32.48 |
| Urban land % 1 km | 4.96 ± 0.79 | 0.68 | 10.64 |
| Urban land % 500 m | 4.40 ± 1.76 | 0.00 | 29.01 |
| Urban land % 250 m | 3.15 ± 1.34 | 0.00 | 19.23 |
| Uncropped land % 1 km | 15.58 ± 0.81 | 11.45 | 20.69 |
| Uncropped land % 500 m | 14.38 ± 0.43 | 11.81 | 17.20 |
| Uncropped land % 250 m | 13.05 ± 1.40 | 5.59 | 25.46 |

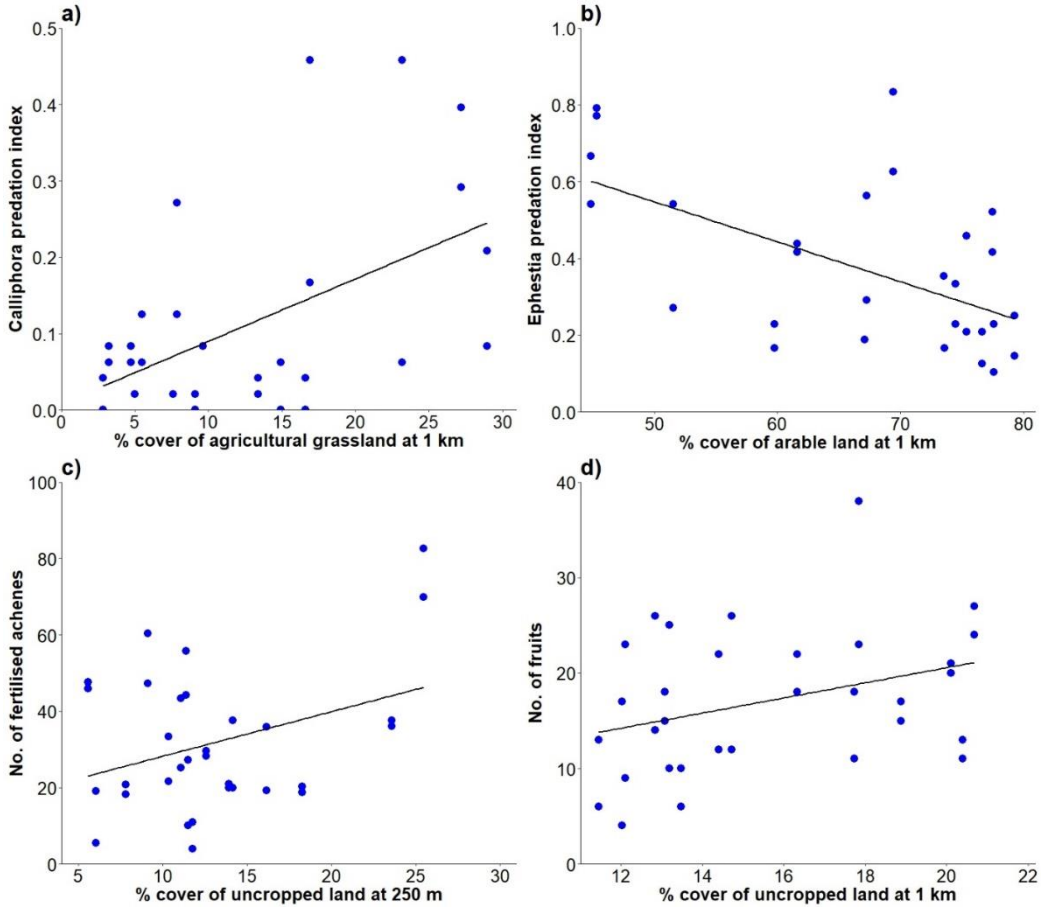


**Figure 4.1.** (a) Effect of the % cover of agricultural grassland at 1 km on *Calliphora* predation; (b) effect of the % cover of arable land at 1 km on *Ephestia* predation; (c) effect of the % cover of uncropped land at 250 m on the number of fertilised achenes produced; and, (d) effect of the % cover of uncropped land at 1 km on the number of strawberry fruits produced.

**Table 4.3.** Results from LMs analysing the effect landscape composition metrics on (a) pest control and (b) pollination metrics measured adjacent to field margin plots. All predictor variables retained in the minimum model are included; ****P* <0.001, ***P* <0.01, **P* <0.05.

| Response variable | Landscape metric | d.f. | *F* | *P* |
|---|---|---|---|---|
| *a) Pest control* | | | | |
| Calliphora predation index | Agricultural grassland % 1 km | 1, 30 | 8.79 | ** (+) |
| Ephestia predation index | Arable % 1 km | 1, 30 | 13.73 | *** (-) |
| *b) Pollination* | | | | |
| No. of fertilised achenes | Agricultural grassland % 250 m | 1, 29 | 8.87 | ** (-) |
| | Uncropped % 250 m | 1, 29 | 7.85 | ** (+) |
| No. of fruits | Uncropped % 1 km | 1, 30 | 5.18 | * (+) |

In contrast, *Ephestia* predation decreased as the proportion of arable land at 1 km increased (Table 4.3a; Figure 4.1b). During the phytometer assay, the number of fertilised achenes produced was negatively affected by the proportion of agricultural grassland at 250 m (Table 4.3b), but positively affected by the proportion of uncropped land at 250 m (Table 4.3b; Figure 4.1c). Furthermore, the proportion of uncropped land at 1 km had a small but significant positive effect on the number of strawberry fruits produced (Table 4.3b; Figure 4.1d).

### 4.3.2. Invertebrate ecosystem service providers

Landscape composition influenced four out of the seven invertebrate ecosystem service provider variables tested (Table 4.4). For these response variables, landscape composition metrics measured at 1 km and 250 m were of equal importance (Table 4.4). Landscape composition had the greatest effect on natural enemies, whereas crop pests were unaffected by landscape composition (Table 4.4). Aerial and canopy-active natural enemies were influenced by landscape composition at 1 km (Table 4.4a, c), but epigeal natural enemies were influenced by landscape composition at 250 m (Table 4.4b).

**Table 4.4.** Results from LMs and GLMs analysing the effect landscape composition metrics on the abundance of invertebrate ecosystem service providers recorded during (a) transect, (b) pitfall trap and (c) sweep net surveys. All predictor variables retained in the minimum model are included; ****P* <0.001, ***P* <0.01, **P* <0.05.

| Response variable | Landscape metric | d.f. | $\chi^2$ | *F* | *P* |
|---|---|---|---|---|---|
| *a) Transects* | | | | | |
| Crop pollinators | Survey season x Arable % 250 m | 2 | 72.59 | | *** |
| Aerial natural enemies | Survey season | 1, 77 | | 39.89 | *** |
| | Arable 1 km | 1, 77 | | 4.57 | * (+) |
| Aerial crop pests | Survey season | 1 | 35.25 | | *** |
| *b) Pitfall trapping* | | | | | |
| Epigeal natural enemies | Uncropped % 250 m | 1 | 7.19 | | ** (-) |
| Epigeal crop pests | No significant factor | | | | |
| *c) Sweep netting* | | | | | |
| Canopy-active natural enemies | Sweep net position | 2 | 30.84 | | *** |
| | Agricultural grassland % 1 km | 1 | 10.57 | | ** (-) |
| Canopy-active crop pests | Sweep net position | 2 | 56.18 | | *** |

During transect surveys within field margin plots, the interaction between survey season and the proportion of arable land at 250 m had a highly significant effect (P <0.001) on the abundance of crop pollinators (Table 4.4a): it had a positive effect on crop pollinators during both survey seasons, but the effect was much greater during late season transects (Figure 4.2a). The abundance of aerial natural enemies also increased as the proportion of arable land at 1 km increased (Table 4.4a; Figure 4.2b).

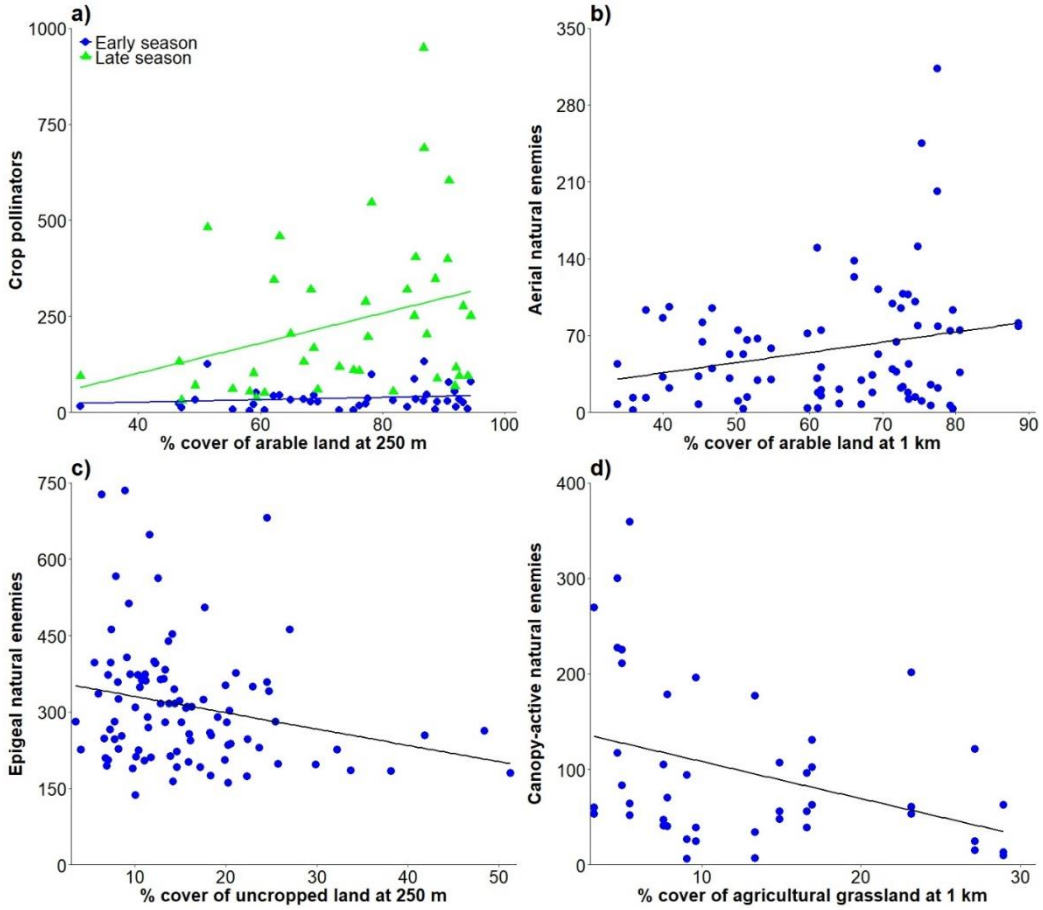


**Figure 4.2.** (a) Effect of the % cover of arable land at 250 m on the abundance of crop pollinators during different transect survey seasons; (b) effect of the % cover of arable land at 1 km on the abundance of aerial natural enemies recorded during transects; (c) effect of the % cover of uncropped land at 250 m on the abundance of epigeal natural enemies caught during pitfall trapping; and, (d) effect of % cover of agricultural grassland at 1 km on the abundance of canopy-active natural enemies caught during sweep net surveys.

During pitfall trapping, landscape composition only affected the abundance of epigeal natural enemies (Table 4.4b), which decreased as the proportion of uncropped land at 250 m increased (Figure 4.2c). During sweep net surveys the proportion of agricultural grassland at 1 km had a negative effect on the abundance of canopy-active natural enemies (Table 4.4c; Figure 4.2d), but no landscape composition metrics remained in the final model for canopy-active crop pests (Table 4.4c).

### 4.3.3. Invertebrate biodiversity

Landscape composition metrics only affected three of the nine biodiversity response variables tested (Table 4.5). Lepidoptera abundance and richness, bumblebee richness, hoverfly abundance and richness, and sweep net taxonomic richness were all unaffected by landscape composition (Table 4.5). Conversely, bumblebee abundance, transect taxonomic richness and pitfall trap taxonomic richness were all affected by landscape composition metrics at 1 km.

**Table 4.5.** Results from LMs and GLMs analysing the effect landscape composition metrics on invertebrate biodiversity metrics recorded during (a) transect, (b) pitfall trap and (c) sweep net surveys. All predictor variables retained in the minimum model are included; ***$P$ <0.001, **$P$ <0.01, *$P$ <0.05.

| Response variable | Landscape metric | d.f. | $\chi^2$ | $F$ | $P$ |
|---|---|---|---|---|---|
| *a) Transects* | | | | | |
| Lepidoptera abundance | Survey season | 1 | 65.85 | | *** |
| Lepidoptera richness | Survey season | 1 | 85.35 | | *** |
| Bumblebee abundance | Survey season | 1 | 32.19 | | *** |
| | Season x % Agricultural grassland 1 km | 2 | 9.79 | | ** |
| Bumblebee richness | Survey season | 1 | 46.63 | | *** |
| Hoverfly abundance | Survey season | 1 | 52.39 | | *** |
| Hoverfly richness | Survey season | 1 | 48.50 | | *** |
| Invertebrate richness | Survey season | 1, 76 | | 26.19 | *** |
| | % Urban 1 km | 1, 76 | | 9.16 | ** (+) |
| | % Agricultural grassland 1 km | 1, 76 | | 4.82 | * (-) |
| *b) Pitfall trapping* | | | | | |
| Invertebrate richness | % Uncropped 1 km | 1,94 | | 8.89 | ** (-) |
| *c) Sweep netting* | | | | | |
| Invertebrate richness | Sweep net position | 2 | | 59.06 | *** |

During transect surveys, the interaction between survey season and the proportion of agricultural grassland at 1 km had a highly significant effect on bumblebee abundance (Table 4.5a): during both survey seasons the proportion of agricultural grassland at 1 km had a negative effect on bumblebee abundance, but the effect was greater during late season transects (Figure 4.3a). Taxonomic richness recorded during transect surveys was affected by the proportion of urban land and agricultural grassland at 1 km (Table 4.5a): the proportion of urban land at 1 km had a positive effect (Table 4.5a; Figure 4.3b), whereas the proportion of agricultural grassland at 1 km had a negative effect (Table 4.5a; Figure 4.3c). During pitfall trapping, taxonomic richness increased as the proportion of uncropped land at 1 km increased (Table 4.5b; Figure 4.5c).

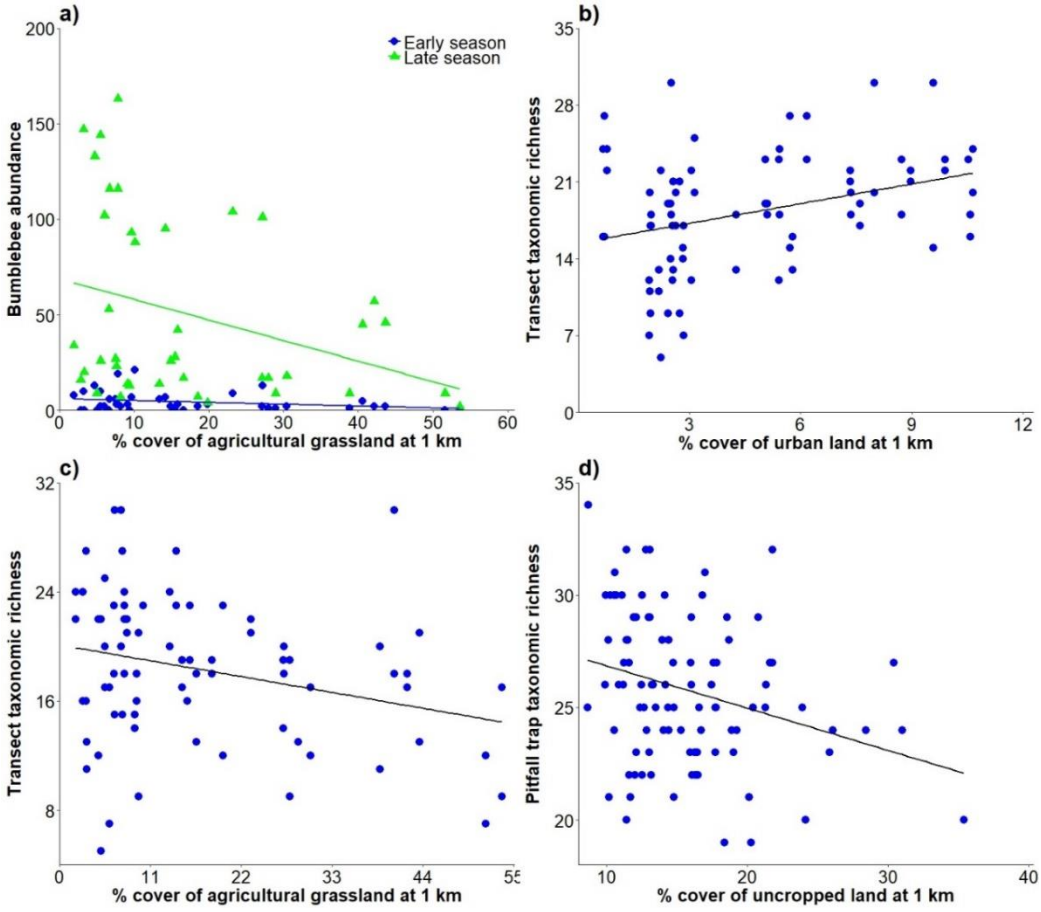


**Figure 4.3.** (a) Effect of the % cover of agricultural grassland at 1 km on bumblebee abundance during different transect survey seasons; (b) effect of the % cover of urban land at 1 km on transect invertebrate richness recorded during transect surveys; (c) effect of the % cover of agricultural grassland at 1 km on transect invertebrate richness recorded during transect surveys; and, (d) effect of the % cover of uncropped land at 1 km on pitfall trap invertebrate richness.

### 4.4 Discussion

Landscape composition is known to be an important factor for supporting and enhancing invertebrate biodiversity and ecosystem services on intensive farmland (Chaplin-Kramer et al., 2011, Kennedy et al., 2013, Shackelford et al., 2013, Veres et al., 2013). However, research in this area has primarily focussed on the response of invertebrates and ecosystem services to the proportion of uncropped land, whilst ignoring the effect of other biotopes (but see Hendrickx et al., 2007, Carre et al., 2009). The present study found that: (i) landscape composition had a significant effect on 11 out of 22 invertebrate and ecosystem service response variables tested (50%); (ii) individual invertebrate taxa and ecosystem services were often influenced by different biotope types, but where the same biotope influenced multiple response variables, the effects were contradictory and/or operated at different spatial scales; (iii) the proportion of agricultural grassland was entered into more models than any other landscape metric and, in most cases, it had a negative effect; and, (iv) in terms of spatial scale, invertebrate taxa and ecosystem services were primarily influenced by landscape composition at 1 km. It is important to note that there were strong correlations between agricultural grassland and arable land at every spatial scale (Pearson correlations between 0.794 and 0.949; see Table A5 in the Appendix). Correlation between landscape composition metrics is a recurrent problem in landscape ecology (Fuentes-Montemayor et al., 2011, Fuentes-Montemayor et al., 2012, Duflot et al., 2015), and the approach of rejecting colinear variables with the lowest $R^2$ value, whilst practical, may have concealed important relationships. Moreover, the correlative approach used here to explore relationships between landscape composition and ecosystem services makes it difficult to imply causality (Shipley, 2016).

#### 4.4.1. Pest control and pollination

Pest control services were strongly influenced by the proportion of agricultural biotopes at 1 km, with *Ephestia* predation being reduced as the proportion of arable land increased and *Calliphora* predation being enhanced as the proportion of agricultural grassland increased. The negative relationship between arable land and *Ephestia* predation is consistent with the findings of Rusch et al. (2016b), who, after conducting a quantitative synthesis of 15 studies, found that a relative increase in arable land at 1 km from 2-100% reduced the level of natural pest control in crop fields by 46%. Landscapes dominated by arable land generally contain a small amount of uncropped land (Robinson and Sutherland, 2002, Tscharntke et al., 2002). At the landscape level, this may reduce natural pest control by limiting the amount of alternative

prey, overwintering sites and shelter (*i.e*. habitat resources) that are crucial for maintaining predatory arthropod populations (Landis et al., 2000, Duelli and Obrist, 2003, Bianchi et al., 2006, Tscharntke et al., 2007). Natural pest control may be further reduced by Insecticide use (Roubos et al., 2014), which is positively correlated with the relative proportion of arable land (Meehan et al., 2011).

In this study, agricultural grasslands were classified as being grazed and/or cut for silage, but increased grazing pressure and cutting frequency can reduce predatory arthropod populations (Haysom et al., 2004, Sjodin et al., 2008, Prieto-Benitez and Mendez, 2011). The positive effect of agricultural grassland on *Calliphora* predation therefore seems counterintuitive. However, the level of grazing intensity (stocking units) or cutting frequency (number of cuts per year) within grasslands was not recorded during landscape mapping. As such, it is possible that a large proportion of grasslands classified as 'agricultural' were low intensity (i.e. low grazing pressure and/or cutting frequencies). If so, they would be more akin to resource-rich uncropped land and thus infer a positive influence on *Calliphora* predation by augmenting natural enemy populations within the landscape (Koh and Holland, 2015). Notwithstanding this possibility, compared to arable land, even the most intensive grasslands are likely to benefit natural pest control because they are less disturbed by farming activities such as ploughing and insecticide use (Herzog et al., 2006), and support a more diverse plant community (Robinson and Sutherland, 2002, Werling et al., 2011, Werling et al., 2014, Cole et al., 2017). For example, Werling et al. (2014) found that perennial (*i.e.* low disturbance) agricultural grasslands harboured significantly greater predatory arthropods and promoted higher levels of pest suppression than cultivated (*i.e.* high disturbance) arable land, with the former also supporting a more diverse plant community. This perhaps suggests that, regardless of intensity, pest control services will be enhanced in landscapes comprised of a greater proportion of grassland relative to arable land.

Results from the phytometer assay revealed that the proportion of uncropped land at 250 m and 1 km had a positive effect on the number of fertilised achenes and fruits produced, respectively. The positive effect of uncropped land on pollination has been documented elsewhere (Kremen et al., 2004, Klein et al., 2012, Bukovinszky et al., 2017, Dainese et al., 2017, Sutter et al., 2017a), but this is the first study to demonstrate the effect of uncropped land on pollination at multiple spatial scales. Strawberry flowers are mainly pollinated by bumblebees and solitary bees (Klatt et al., 2014, Rader et al., 2016, Ellis et al., 2017). Due to differences in flight ranges, solitary bees are more likely to be enhanced by landscape composition at small spatial scales <500 m (Gathmann and Tscharntke, 2002, Steffan-

Dewenter, 2002, Holzschuh et al., 2010, Steckel et al., 2014), whilst bumblebees are more likely to be enhanced by landscape composition at medium to large spatial scales >500 m (Knight et al., 2005, Osborne et al., 2008a, Carvell et al., 2012, Holland et al., 2015, Wood et al., 2015c). Such taxa-specific responses to landscape composition could explain the multi-scale response to uncropped land. Alternatively, a greater proportion of uncropped land at 250 m may have increased the number of visits to phytometers by elevating local densities of flower-visiting insects (Ricketts, 2004, Garibaldi et al., 2011, Blaauw and Isaacs, 2012, Blaauw and Isaacs, 2014b, Sutter et al., 2017a). This seems likely because, whilst the floral resources within uncropped land were not quantified, it generally contains a greater abundance and richness of flowers than found in agricultural biotopes (Kells et al., 2001, Carvell et al., 2007, Osborne et al., 2008b, Lye et al., 2009, Cole et al., 2017). At larger spatial scales (*e.g.* 1 km), the presence of uncropped land should enhance pollination by increasing absolute numbers of flower-visitors in the surrounding landscape because of a greater availability of food resources (Carvell et al., 2015, Jonsson et al., 2015, Wood et al., 2015c, Bukovinszky et al., 2017, Häussler et al., 2017).

In contrast to the positive effect of uncropped land, the proportion of agricultural grassland at 250 m had a negative effect on the number of fertilised achenes produced. In a given patch of uncropped land, pollinator densities can be diluted when other patches in the surrounding landscape contain a greater concentration of floral resources (Holzschuh et al., 2011, Holzschuh et al., 2016). It could be that agricultural grasslands provided such a concentration of floral resources, which was superior to the floral resources found within the areas of uncropped land immediately adjacent to phytometer locations. If so, then pollination may have been reduced due to reductions in local densities of flower-visiting insects. However, this is unlikely because agricultural grasslands generally provide poor foraging habitat for flower-visiting insects (Potts et al., 2009, Wood et al., 2015a, Cole et al., 2017).

#### 4.4.2. Invertebrate ecosystem service providers

Crop pollinator abundance was enhanced by the proportion of arable land at 250 m during both transect survey seasons, but the strength of this relationship was much greater during late season transects. Arable biotopes local to field margin plots were dominated by cereal crops, which provide little to no floral resources for pollinating insects (*e.g.* occasional weeds) (Werling et al., 2014, Cole et al., 2017). Consequently, a greater proportion of arable land at 250 m would increase the 'ecological contrast' of forb-rich field margins, *i.e.* field margins would provide resources not present in the surrounding landscape and would therefore be

more apparent to flower-visitors (Kleijn et al., 2011), with this contrast being much larger during late season transect surveys when significantly more species were in flower (see §3.3.2). There is accruing evidence that such landscape-level ecological contrasts increase the abundance and density of pollinating insects found within forb-rich patches of uncropped land (*e.g.* field margins) (Heard et al., 2007, Haenke et al., 2009, Carvell et al., 2011, Scheper et al., 2013, Haenke et al., 2014, Scheper et al., 2015).

Across all invertebrate surveys, crop pests remained unaffected by landscape composition. There are several possible explanations for this finding. One is that crop pests may respond to aspects of landscape composition other than those investigated here. During sweep net and transect surveys, pollen beetles (Nitidulidae) were the dominant crop pest, but the most important factor driving pollen beetle abundance within agro-ecosystems is the proportion of oilseed rape grown during the previous year (Rusch et al., 2012, Skellern et al., 2017), which was not quantified in the present study. However, it is more likely that the effect of landscape composition on transect and sweep net crop pests was overridden by the influence of margin quality, transect survey season and sweep net position (see §3.3.3.2). Regarding epigeal crop pests, it is well established that pitfall traps measure invertebrate activity rather than true abundance, with trap catches being determined by local food resources and vegetation structure (Adis, 1979, Sunderland, 1995, Melbourne, 1999, Lang, 2000). And so, the numbers of epigeal crop pests caught during pitfall trapping may reflect the variation in local conditions, rather than the proportion of different biotopes in the surrounding landscape.

Compared to crop pests, natural enemies displayed a strong response to landscape composition, but individual guilds (*e.g.* aerial, canopy-active and epigeal) were affected by different biotope types. For example, aerial natural enemies were enhanced by the proportion of arable land at 1 km, which, similar to crop pollinators, probably reflects the ecological contrast provided by forb-rich field margin plots within landscapes dominated by arable fields (Haenke et al., 2009, Haenke et al., 2014). Conversely, canopy-active natural enemies responded negatively to increasing proportions of agricultural grassland at 1km. Whilst it is unlikely that agricultural grasslands provide sufficient flowers to draw natural enemies away from uncropped areas (Potts et al., 2009, Cole et al., 2017), they may support other resources in sufficient quantities to do so (*e.g.* prey/hosts) (Werling et al., 2011, Werling et al., 2014). In the latter case, densities of natural enemies within uncropped areas would be reduced in landscapes comprised of greater proportions of agricultural grassland (*i.e.* via dilution *sensu* (Holzschuh et al., 2011, Holzschuh et al., 2016). Interestingly, increasing

proportions of uncropped land at 250 m reduced the number of epigeal natural enemies within margin plots. Many epigeal natural enemies, such as carabid beetles and spiders, appear to be adapted to agricultural biotopes (Coombes and Sotherton, 1986, Schmidt et al., 2008, Flohre et al., 2011, Winqvist et al., 2011, Rusch et al., 2016a, Dainese et al., 2017), which provide them with a greater availability of habitat resources than uncropped land (Holland et al., 2004, Holland et al., 2005, Rand et al., 2006, Rand and Tscharntke, 2007). Epigeal natural enemies may therefore be more abundant in landscapes comprised of small patches of uncropped land surrounded by agricultural biotopes.

#### 4.4.3. Invertebrate biodiversity

In contrast to previous work (Krauss et al., 2003, Heard et al., 2007, Rundlöf et al., 2008b, Haenke et al., 2009, Meyer et al., 2009, Carvell et al., 2011, Holland et al., 2015, Wood et al., 2015a), landscape composition had no effect on Lepidoptera abundance or richness, hoverfly abundance or richness, and bumblebee richness. The results presented in Chapter 2 (§3.3.3.3) and unreported results in the current chapter (§4.3) suggest that the influence of other factors, such as margin quality and transect survey season, probably masked the effect of landscape composition. On the other hand, landscape composition had a significant effect on bumblebee abundance, and taxonomic richness during transects and pitfall trapping. The positive response of invertebrate richness during transects to the proportion of urban land at 1 km could be due to a greater presence of gardens, farm buildings and brownfield sites in the surrounding landscape, as these areas are known to support diverse invertebrate communities owing to their provision of important habitat resources (Cane et al., 2006, Osborne et al., 2008b, Carre et al., 2009, Owen, 2010, Jones and Leather, 2012, Baldock et al., 2015, Sirohi et al., 2015).

Taxonomic richness during transects also responded to the proportion of agricultural grassland at 1 km, as did bumblebee abundance, and in both cases, it had a negative effect. However, for bumblebees, the effect of agricultural grassland interacted with season, with a much stronger effect apparent during late season transect surveys. Cole et al. (2017) found that hedgerows, field margins and road verges (*viz.* uncropped land) contain a greater abundance and diversity of flowers than agricultural grasslands. Furthermore, an increase in landscape-wide floral resources can enhance bumblebee populations (Carvell et al., 2015, Wood et al., 2015c, Carvell et al., 2017). Thus, landscapes comprised of a greater proportion of forb-poor grasslands probably support lower absolute numbers of bumblebees. So, one would expect a decrease in bumblebee abundance as the proportion of agricultural grassland

increased, with this effect being more apparent during late season transects when more pollinators are active (see §3.3.3.3). As most individuals recorded during transects were flower-visitors, it is likely that transect invertebrate richness is responding to agricultural grassland in the same way.

Finally, the proportion of uncropped land at 1 km had a negative effect on the richness of invertebrate taxa recorded during pitfall trapping. Within intensive agro-ecosystems, like the farms used in this study, the epigeal invertebrate community is likely to consist of taxa that can tolerate intensive cropping systems and grassland (Schmidt et al., 2008, Gamez-Virues et al., 2015, Gossner et al., 2016), especially given the low dispersal ability of many epigeal invertebrates (Thomas et al., 1997, Holland et al., 2004, Holland et al., 2005). These taxa may only require small patches of uncropped land to survive because many of their habitat resources are obtained from the crop (Rand et al., 2006, Rand and Tscharntke, 2007). Consequently, the richness of epigeal invertebrates on intensive farmland may increase with decreasing amounts of uncropped land. To the authors knowledge, this is the first study to find such a relationship.

#### 4.4.4. Landscape management trade-offs and synergies

In terms of landscape management prescriptions, the most relevant findings of this study were twofold. First, individual invertebrate taxa and ecosystem services were largely influenced by different biotope types, but when several services and/or taxa were influenced by the same biotope, the effects were contradictory and/or operated at different scales (Table 4.6). Second, uncropped land was relatively unimportant: it only remained in four out of the 11 models where landscape composition was significant and in two of these models it had a negative effect (Table 4.6). In contrast to previous studies (Shackelford et al., 2013, Dainese et al., 2017, Sutter et al., 2017a), this suggests that landscape management to promote multiple ecosystem service and biodiversity benefits cannot be achieved by just increasing the amount of uncropped land. It appears that the best approach would be to increase the compositional complexity of landscapes (*i.e.* increase the diversity of biotope types) at the farm (1 km) level, but more work is required to validate this management option. Alternatively, the contradictory effects of agricultural grassland and arable land on different services may be because they were strongly colinear at every spatial scale (see Table A5). Lastly, agricultural grassland remained in more models than any other biotope metric (5 out of the 11 significant landscape models), where it tended to have a negative effect (Table 4.6). The reason for this was unclear and therefore requires further investigation.

**Table 4.6.** A summary table showing the significant relationships recorded between landscape composition metrics and biodiversity/ecosystem service response variables.

| Response variable | Arable land % | | Agricultural grassland % | | Urban % | Uncropped land % | |
|---|---|---|---|---|---|---|---|
| | 1 km | 250 m | 1 km | 250 m | 1 km | 1 km | 250 m |
| *Calliphora* predation | | | + | | | | |
| *Ephestia* predation | - | | | | | | |
| No. of fertilised achenes | | | | - | | | + |
| No. of fruits produced | | | | | | + | |
| Crop pollinators | | + | | | | | |
| Aerial natural enemies | + | | | | | | |
| Epigeal natural enemies | | | | | | | - |
| Canopy-active natural enemies | | | - | | | | |
| Bumblebee abundance | | | - | | | | |
| Transect invertebrate richness | | | - | | + | | |
| Pitfall trap invertebrate richness | | | | | | - | |

## 4.5 Conclusion

In summary, landscape composition had a significant effect on 50% of the invertebrate biodiversity and ecosystem service response variables tested. Pest control, pollination, natural enemies and crop pollinators displayed strong responses to landscape composition, whereas crop pests and two-thirds of the biodiversity variables tested were unaffected. Different biotopes and spatial scales were important for different taxa and services, which suggests that increasing the compositional complexity of landscapes at several spatial scales might be the best management approach for achieving multiple ecosystem service and biodiversity benefits, but more work is required to confirm this.

# Chapter 5: Exploring the effect of landscape complexity and functional habitat connectivity on invertebrate biodiversity and ecosystem service provision within arable field margins

**5.1 Introduction**

Agriculture occupies 71% of the UK land area (DEFRA, 2016b). Not only does this mean that agricultural landscapes support most of the UKs biodiversity and ecosystem services (Krebs et al., 1999, Firbank et al., 2013), but also that the total conservation potential of farmland may exceed that of nature reserves (Bignal, 1998, Altieri, 1999, Krebs et al., 1999, Hayhow et al., 2016). Yet, farmland invertebrates and the ecosystem services they provide currently face a multitude of threats associated with intensive agriculture (e.g. Biesmeijer et al., 2006, Potts et al., 2010, Carvalheiro et al., 2013, Hayhow et al., 2016). Two of the most pervasive threats are landscape simplification and habitat fragmentation, *i.e.* the widespread transformation of agro-ecosystems into landscapes characterised by large uniform crop fields (landscape simplification) interspersed with small and highly fragmented patches of uncropped land (habitat fragmentation) (Burel, 1996, Robinson and Sutherland, 2002, Benton et al., 2003, Fahrig, 2003).

Landscape simplification and habitat fragmentation threaten farmland invertebrate populations in several ways. Firstly, habitat fragmentation reduces the number of suitable/available habitat patches and the connectivity between them (Debinski and Holt, 2000, Dover and Settele, 2009). Areas of uncropped land within agro-ecosystems provide many invertebrate species with crucial habitat resources that are often absent from crop fields (Landis et al., 2000, Bianchi et al., 2006, Cole et al., 2017, Gurr et al., 2017). Within highly fragmented agricultural landscapes, the distances between these resource-rich areas may be large (Fahrig, 2003, Ockinger and Smith, 2007), which would inhibit inter-patch transfers (Steffan-Dewenter and Tscharntke, 1999, Tscharntke et al., 2002, Rösch et al., 2013) and, in extreme cases, lead to the isolation of invertebrate populations (Ricketts, 2001, Thomas et al., 2001, Ockinger et al., 2010, Knapp and Rezac, 2015). Furthermore, even if a species is capable of traversing large distances, it may hesitate to do so if it must cross unsuitable habitat (*i.e.* areas that are resource poor) (Dover, 1990, Saunders et al., 1991, Dover and Settele, 2009). Once isolated, the likelihood of an invertebrate population becoming extinct will increase due to insufficient resources on the natal patch (*e.g.* via competition for resources), inbreeding depression, reduced gene flow and a greater vulnerability to stochastic events (e.g. Wissel et al., 1994, Nieminen et al., 2001, Keller and Largiadèr, 2003, Frank, 2005).

Secondly, landscape simplification has reduced the diversity of biotopes present within agro-ecosystems (Robinson and Sutherland, 2002, Benton et al., 2003), *i.e.* landscapes have reduced compositional complexity (Fahrig et al., 2011). Whilst many farmland invertebrate species depend on the resources within uncropped land to survive (Duelli and

Obrist, 2003), they will also exploit resources in other biotopes, including crop fields (Harwood et al., 2004, Baldock et al., 2015, Cole et al., 2017). Moreover, certain invertebrate taxa may be more dependent on the resources found in different biotopes than those present in uncropped land (see Tscharntke et al., 2016 and references therein). Thus, agro-ecosystems containing a complex mosaic of biotope types are likely to support a greater number and richness of invertebrates than simplified agro-ecosystems consisting primarily of crop fields (Fahrig et al., 2011), which generally contain a homogenous suite of species adapted to a high-level of disturbance (Ekroos et al., 2010, Flohre et al., 2011, Carvalheiro et al., 2013, Gamez-Virues et al., 2015).

Thirdly, intensive agricultural practices have led to the creation of landscapes dominated by large, uniformly shaped fields (Benton et al., 2003, Kareiva et al., 2007, Fahrig et al., 2015). As such, modern agro-ecosystems contain a low proportion of edge features separating different land-uses, *i.e*. they have reduced structural complexity (Fahrig et al., 2011). However, field edges are extremely important to farmland invertebrates because they receive less intensive management than field centres (Clough et al., 2007) and are often demarcated by a resource rich and sheltered boundary feature (*e.g.* field margin, hedgerow or ditch) (Maudsley, 2000, Marshall and Moonen, 2002, Carvell et al., 2007, Cole et al., 2017), which can act as a dispersal corridor between suitable habitat patches or facilitate the spill-over of beneficial invertebrates into the crop (Holzschuh et al., 2010, Cranmer et al., 2012, Inclán et al., 2016, Woodcock et al., 2016a).

Landscape simplification and habitat fragmentation clearly threaten farmland invertebrate populations, and in doing so they may also degrade agronomically important ecosystem services, such as pest control and pollination (Chaplin-Kramer et al., 2011, Cranmer et al., 2012, Hadley and Betts, 2012, Connelly et al., 2015). Consequently, numerous studies have investigated how the different aspects of landscape simplification and habitat fragmentation affect farmland invertebrates and the provision of ecosystem services (e.g. Chaplin-Kramer et al., 2011, Garibaldi et al., 2011, Rusch et al., 2013a, Shackelford et al., 2013). Concerning landscape simplification, most studies have focussed on the impact of compositional landscape complexity, which, in general, has a positive effect on farmland invertebrate biodiversity and abundance (Steckel et al., 2014, Perovic et al., 2015), but also increases the delivery of pest control and pollination services (Chaplin-Kramer et al., 2011, Andersson et al., 2014, Connelly et al., 2015, Rusch et al., 2016b). Yet, a large proportion of these studies use either the proportion of arable land (e.g. Winqvist et al., 2011) or the proportion uncropped land (e.g. Bukovinszky et al., 2017) as proxy measurements of

compositional landscape complexity. Therefore, there are relatively few studies that have used true measures of compositional complexity, such as the Shannon or Simpson diversity index of landcover types (but see Gardiner et al., 2009, Fuentes-Montemayor et al., 2011, Steckel et al., 2014, Perovic et al., 2015).

In contrast, studies investigating the effect of structural landscape complexity on farmland invertebrates are few (but see Holzschuh et al., 2010, Kennedy et al., 2013, Steckel et al., 2014), and, as far as the author is aware, there are none that examine its effect on invertebrate ecosystem service provision. Nevertheless, where it has been investigated, structural complexity at the landscape-scale has mixed effects on invertebrate biodiversity (Steckel et al., 2014). For example, Kennedy et al. (2013) found weak effects of structural complexity on bees in a study spanning 39 crop systems globally. Conversely, Steckel et al. (2014) found that the abundance and richness of cavity nesting bee and wasp antagonists increased in landscapes comprised of more complex patch shapes.

Habitat fragmentation studies within agro-ecosystems have primarily focussed on how the distance to/between source habitats or the structural connectivity between habitats effects invertebrate populations and the ecosystem services they provide (e.g. Steffan-Dewenter and Tscharntke, 1999, Hendrickx et al., 2007, Rösch et al., 2013, Haenke et al., 2014). Overall, these studies suggest that increases in distance to/between source habitats and reductions in structural connectivity between habitats has a negative effect on the abundance and richness of invertebrates, and the provision of pest control and pollination services (Steffan-Dewenter and Tscharntke, 1999, Van Geert et al., 2010, Cranmer et al., 2012, Schüepp et al., 2014). The effects of habitat fragmentation can also be measured using functional habitat connectivity (Tischendorf and Fahring, 2000, Fischer and Lindenmayer, 2007), which differs from physical habitat connectivity in that the latter is equated with habitat patch contiguity (*i.e.* patches are physical/structurally connected), whereas the former considers habitat patches 'connected' if the distance separating them is below a given threshold that is taxa/species specific (Tischendorf and Fahring, 2000, McGarigal et al., 2002, Uezu et al., 2005, Dennis et al., 2013). Thus, in rare cases (*e.g.* for species that will not traverse any amount of non-habitat), functional connectivity can be the same as physical connectivity (*i.e.* the threshold distance is zero) (Tischendorf and Fahring, 2000, Dennis et al., 2013). But when considering farmland invertebrates, patches of uncropped land separated by up to 25 metres are likely to be functionally 'connected' because most taxa can traverse this distance (e.g. Thomas et al., 2003, Holland et al., 2004, Cant et al., 2005, Osborne et al., 2008a, Zurbuchen et al., 2010). Indeed, for some taxa (e.g. bumblebees), habitat patches would be

functionally connected when separated by distances over 400 m (Knight et al., 2005). Given that is often impractical for farmers to physically connect patches of uncropped land at the landscape-scale, functional habitat connectivity represents a more practical solution to ameliorating the negative effects of habitat fragmentation on farmland invertebrate populations. However, to date, its effect on invertebrate biodiversity and ecosystem service provision remains unexplored.

The present study investigated how landscape complexity (compositional and structural) and functional habitat connectivity influence farmland invertebrate populations and the ecosystem services they provide. Landscape complexity and functional connectivity metrics were assessed within 1 km, 500 m and 250 m radii surrounding the same field margin plots in which a range of invertebrate biodiversity and ecosystem service response variables were measured. Using this data, we explored the effect of landscape complexity and functional habitat connectivity on: (i) the delivery of pest control and pollination services; (ii) the abundance of invertebrate ecosystem dis/service providers; and, (iii) the amount of invertebrate biodiversity. This study will further expand our understanding of the mechanisms driving landscape effects on invertebrate biodiversity and ecosystem service provision on farmland.

**5.2 Data Analysis**

Please refer to Chapter 2 for detailed study design and data collection information. Linear and generalised linear models (LMs and GLMs, respectively) were used to analyse the relationships between landscape complexity, functional habitat connectivity and: (i) pest control and pollination services; (ii) the abundance of crop pollinators, natural enemies and crop pests; and, (iii) invertebrate biodiversity (Table 5.1). Because the specific focus of this chapter was to examine the influence of landscape complexity and functional habitat connectivity on the response variables listed in Table 5.1, margin quality was not included as a fixed effect in any of the models tested. As soil ecosystem services are unlikely to be influenced by either landscape complexity or habitat connectivity, they were not included in the analysis. All statistical procedures within this chapter were performed using R v3.2.2 (R Development Core Team, 2016). LMs and GLMs were validated by visually inspecting residual plots and applying Shapiro-Wilk tests to check the distribution of residuals, homogeneity of variance and model mis-specification (Zuur et al., 2009, Crawley, 2012). A full list of the LMs and GLMs, model

error structures and data transformations used in this chapter can be found in Table A6 within the Appendix.

**Table 5.1.** (a) Pest control, (b) pollination, (c) invertebrate ecosystem service provider and (e) invertebrate biodiversity response variables used during analysis. The table also shows how and where each variable was measured.

| Response variables | Survey | Measurement location |
|---|---|---|
| *a) Pest control* | | |
| Calliphora predation index | Field assay | Crop edge and crop interior |
| Ephestia predation index | Field assay | Crop edge and crop interior |
| *b) Pollination* | | |
| No. of fertilised achenes | Field assay | Crop edge and crop interior |
| No. of fruits | Field assay | Crop edge and crop interior |
| *c) Invertebrate ecosystem service providers* | | |
| Aerial natural enemy abundance | Transects | Margin |
| Aerial crop pest abundance | Transects | Margin |
| Epigeal natural enemy abundance | Pitfall trapping | Margin |
| Epigeal crop pest abundance | Pitfall trapping | Margin |
| Canopy-active natural enemy abundance | Sweep netting | Margin, crop edge and crop interior |
| Canopy-active crop pest abundance | Sweep netting | Margin, crop edge and crop interior |
| *d) Invertebrate biodiversity* | | |
| Lepidoptera abundance | Transects | Margin |
| Lepidoptera richness | Transects | Margin |
| Bumblebee abundance | Transects | Margin |
| Bumblebee richness | Transects | Margin |
| Hoverfly abundance | Transects | Margin |
| Hoverfly richness | Transects | Margin |
| Taxonomic richness | Transects | Margin |
| Taxonomic richness | Pitfall trapping | Margin |
| Taxonomic richness | Sweep netting | Margin, crop edge and crop interior |

The effect of landscape complexity and functional habitat connectivity were assessed within 1km, 500 m and 250 m radii surrounding each field margin plot using three metrics representing different aspects of landscape complexity and habitat connectivity: (i) Shannon biotope diversity index (SHBDI, used as a measure of compositional landscape complexity); (ii) shape index (used as a measure of structural landscape complexity); and, (iii) uncropped connectance index (used as a measure of functional habitat connectivity). Methodological descriptions of these metrics and justification can be found in Chapter 2 (§2.3). Crop position (pollination and pest control metrics), transect survey season (transect ecosystem service

provider and biodiversity metrics) and sweep net survey position (sweep net ecosystem service provider and biodiversity metrics), as well as their interactions with landscape composition metrics, were also included as fixed effects within initial models (however, only if they passed the $R^2$ and collinearity selection process described below). As the main effects of these predictor variables have already been explored in Chapter 3 (see §3.3), only their interactions with landscape metrics are discussed herein.

To avoid overfitting, predictor variables were only included in starting models if they had an $R^2$ value of >0.05. Collinearity between predictor variables was determined by using variance inflation factor and Pearson correlation coefficient thresholds of <3 and <0.65, respectively (Zuur et al., 2009, Zuur et al., 2010). When selected variables exceeded these thresholds, the variables with the lowest $R^2$ values were rejected (see Table A7 in the Appendix for correlation matrices of landscape metrics). Models were simplified using a backward-stepwise deletion procedure from the starting model until only significant predictors ($P$ <0.05) remained (Zuur et al., 2009, Crawley, 2012). At each deletion step, models were assessed using $F$ tests (LMs) or Chi-square tests (GLMs) for a significant increase in residual deviance. If the removal of a non-significant landscape metric significantly increased the residual deviance, it was re-entered into the model (Zuur et al., 2009, Crawley, 2012).

## 5.3 Results

Overall, functional habitat connectivity had no effect on any invertebrate biodiversity or ecosystem service response variables measured. In addition, compositional and structural landscape complexity only influenced two and four biodiversity and ecosystem service response variable, respectively. Across sample farms, landscape configuration metrics varied considerably between farms (Table 5.2). However, there were some general patterns. SHBDI decreased, whereas uncropped connectance increased between 1 km and 250 m (Table 5.2). In contrast, shape index values tended to be highest at 250 m and lowest at 500 m (Table 5.2).

### 5.3.1. Pest control and pollination

Pest control metrics were unaffected by both shape index and uncropped connectance index, but SHBDI at 1 km had a significant positive effect on *Calliphora* and *Ephestia* predation (Table 5.3a; Figure 5.1a, b). Conversely, pollination metrics were unresponsive to any landscape metric (Table 5.3b).

**Table 5.2.** Mean (± SEM), minimum and maximum values for different landscape complexity and connectivity metrics measured within 1 km, 500 m and 250 m radii surrounding margin plots used during (a) transects, (b) pitfall trapping or (c) sweep netting/field assays.

| Biotope class | Mean ± SEM | Minimum | Maximum |
|---|---|---|---|
| *a) Transects* | | | |
| Shannon biotope diversity 1 km | 0.95 ± 0.02 | 0.43 | 1.23 |
| Shannon biotope diversity 500 m | 0.78 ± 0.03 | 0.33 | 1.28 |
| Shannon biotope diversity 250 m | 0.65 ± 0.03 | 0.22 | 1.25 |
| Shape index 1 km | 2.21 ± 0.07 | 1.57 | 4.62 |
| Shape index 500 m | 2.05 ± 0.06 | 1.37 | 4.26 |
| Shape index 250 m | 2.38 ± 0.08 | 1.44 | 4.51 |
| Uncropped connectance index 1 km | 7.59 ± 0.51 | 2.69 | 25 |
| Uncropped connectance index 500 m | 30.28 ± 2.19 | 0.00 | 100 |
| Uncropped connectance index 250 m | 35.34 ± 3.76 | 0.00 | 100 |
| *b) Pitfall trapping* | | | |
| Shannon biotope diversity 1 km | 0.93 ± 0.02 | 0.33 | 1.24 |
| Shannon biotope diversity 500 m | 0.79 ± 0.03 | 0.23 | 1.28 |
| Shannon biotope diversity 250 m | 0.65 ± 0.03 | 0.15 | 1.25 |
| Shape index 1 km | 2.29 ± 0.06 | 1.54 | 4.62 |
| Shape index 500 m | 2.25 ± 0.08 | 1.37 | 4.86 |
| Shape index 250 m | 2.45 ± 0.08 | 1.34 | 4.51 |
| Uncropped connectance index 1 km | 9.08 ± 0.67 | 1.75 | 36.79 |
| Uncropped connectance index 500 m | 31.24 ± 2.19 | 0.00 | 100 |
| Uncropped connectance index 250 m | 37.59 ± 3.50 | 0.00 | 100 |
| *c) Sweep netting/field assays* | | | |
| Shannon biotope diversity 1 km | 0.92 ± 0.03 | 0.65 | 1.23 |
| Shannon biotope diversity 500 m | 0.82 ± 0.04 | 0.39 | 1.28 |
| Shannon biotope diversity 250 m | 0.73 ± 0.06 | 0.22 | 1.25 |
| Shape index 1 km | 2.47 ± 0.15 | 1.78 | 4.62 |
| Shape index 500 m | 2.08 ± 0.13 | 1.37 | 4.26 |
| Shape index 250 m | 2.26 ± 0.09 | 1.49 | 3.25 |
| Uncropped connectance index 1 km | 7.93 ± 0.73 | 2.69 | 15.65 |
| Uncropped connectance index 500 m | 27.60 ± 2.46 | 9.96 | 57.41 |
| Uncropped connectance index 250 m | 41.10 ± 5.46 | 0 | 100 |

**Table 5.3.** Results from LMs analysing the effect landscape complexity metrics and functional habitat connectivity on (a) pest control and (b) pollination metrics measured adjacent to field margin plots. All predictor variables retained in the minimum model are included; ***$P$ <0.001, **$P$ <0.01, *$P$ <0.05.

| Response variable | Landscape metric | d.f. | $F$ | $\chi^2$ | $P$ |
|---|---|---|---|---|---|
| *a) Pest control* | | | | | |
| Calliphora predation index | Shannon biotope diversity 1 km | 1, 30 | 7.74 | | ** (+) |
| Ephestia predation index | Shannon biotope diversity 1 km | 1, 30 | 11.52 | | ** (+) |
| *b) Pollination* | | | | | |
| No. of fertilised achenes | No significant factor | | | | |
| No. of strawberry fruits | No significant factor | | | | |

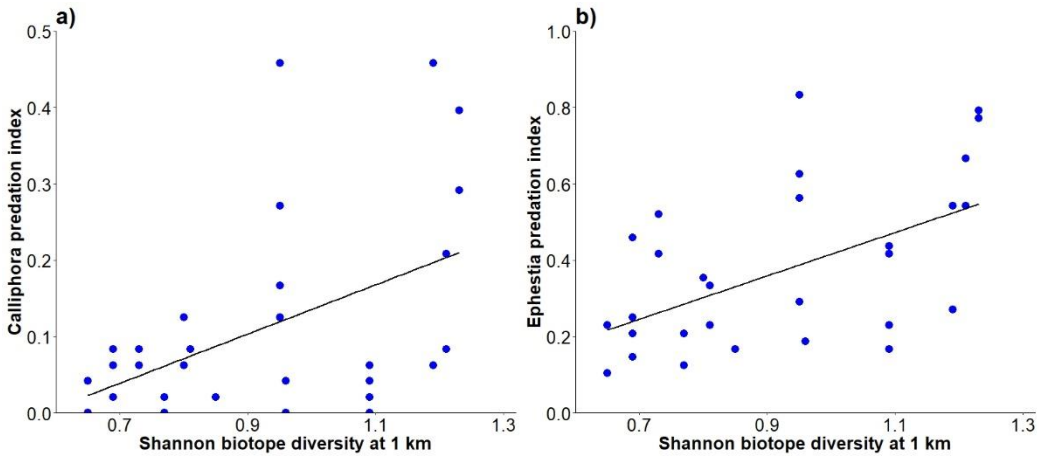


**Figure 5.1.** (a) The effect of Shannon biotope diversity at 1 km on *Calliphora* predation; and, (b) the effect of Shannon biotope diversity at 1 km on *Ephestia* predation.

### 5.3.2. Invertebrate ecosystem service and disservice providers

Uncropped connectance index and SHBDI had no effect on any ecosystem dis/service provider group (Table 5.4). However, shape index had a highly significant ($P$ <0.001) positive effect on aerial and canopy-active natural enemies at 1 km and 500 m, respectively (Table 5.4; Figure 5.2).

### 5.3.3. Invertebrate biodiversity

Invertebrate biodiversity metrics were unaffected by uncropped connectance index and SHBDI, but shape index influenced both hoverfly abundance and transect taxonomic richness (Table 5.5). Shape index at 1 km had a highly significant ($P$ <0.001) positive effect on hoverfly abundance (Table 5.5a; Figure 5.3a), whereas, shape index at 500 m had a small but significant negative effect on transect taxonomic richness (Table 5.5a; Figure 5.3b).

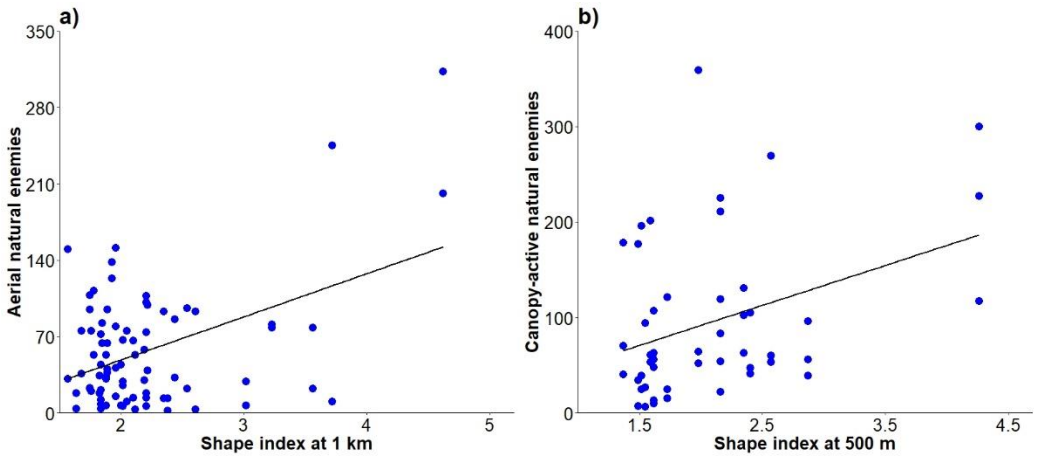


**Figure 5.2.** (a) The effect of shape index at 1 km on the abundance of aerial natural enemies; and, (b) the effect of shape index at 500 m on the abundance of canopy-active natural enemies.

**Table 5.4.** Results from GLMs analysing the effect landscape complexity metrics and functional habitat connectivity on the abundance of invertebrate ecosystem service providers recorded during (a) transect, (b) pitfall trap and (c) sweep net surveys. All predictor variables retained in the minimum model are included; ****P* <0.001, ***P* <0.01, **P* <0.05.

| Response variable | Landscape metric | d.f. | $\chi^2$ | *P* |
|---|---|---|---|---|
| *a) Transects* | | | | |
| Crop pollinators | Survey season | 1 | 66.98 | *** |
| Aerial natural enemies | Survey season | 1 | 23.71 | *** |
| | Shape index 1 km | 1 | 11.54 | *** (+) |
| Aerial crop pests | Survey season | 1 | 35.25 | *** |
| *b) Pitfall trapping* | | | | |
| Epigeal natural enemies | No significant factor | | | |
| Epigeal crop pests | No significant factor | | | |
| *c) Sweep netting* | | | | |
| Canopy-active natural enemies | Sweep net position | 2 | 35.25 | *** |
| | Shape index 500 m | 1 | 16.27 | *** (+) |
| Canopy-active crop pests | Sweep net position | 2 | 56.18 | *** |

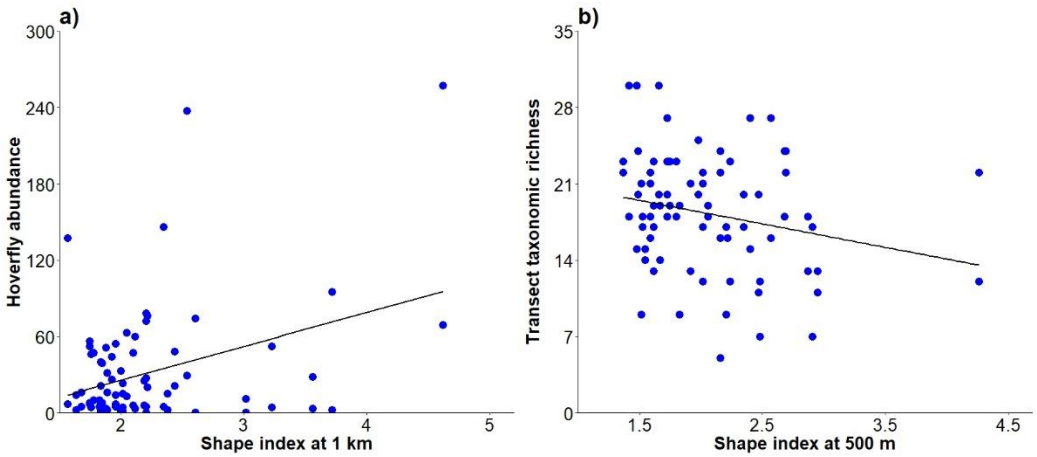


**Figure 5.3.** (a) The effect of shape index at 1 km on hoverfly abundance recorded during transects; and, (b) the effect of shape index at 500 m on invertebrate taxonomic richness recorded during transects.

**Table 5.5.** Results from LMs and GLMs analysing the effect landscape complexity metrics and functional habitat connectivity on invertebrate biodiversity response variables recorded during (a) transect, (b) pitfall trap and (c) sweep net surveys. All predictor variables retained in the minimum model are included; ****P* <0.001, ***P* <0.01, **P* <0.05.

| Response variable | Landscape metric | d.f. | $\chi^2$ | *F* | *P* |
|---|---|---|---|---|---|
| *a) Transects* | | | | | |
| Lepidoptera abundance | Survey season | 1 | 65.85 | | *** |
| Lepidoptera richness | Survey season | 1 | 85.35 | | *** |
| Bumblebee abundance | Survey season | 1 | 62.63 | | *** |
| Bumblebee richness | Survey season | 1 | 46.63 | | *** |
| Hoverfly abundance | Survey season | 1 | 62.13 | | *** |
| | Shape index 1 km | 1 | 17.35 | | *** (+) |
| Hoverfly richness | Survey season | 1 | 48.50 | | *** |
| Taxonomic richness | Survey season | 1, 77 | | 22.87 | *** |
| | Shape index 500 m | 1, 77 | | 5.46 | * (-) |
| *b) Pitfall trapping* | | | | | |
| Taxonomic richness | No significant factor | | | | |
| *c) Sweep netting* | | | | | |
| Taxonomic richness | Sweep net position | 2 | 59.06 | | *** |

## 5.4 Discussion

Numerous studies have documented the positive effect of increased landscape complexity (compositional and structural) and habitat connectivity on invertebrate biodiversity and ecosystem service provision (e.g. Diekotter et al., 2008, Fahrig et al., 2015, Perovic et al., 2015). However, the results of this study suggest that they are relatively unimportant mechanisms driving the abundance of farmland invertebrates and the ecosystem services they provide. For example, the functional connectivity between patches of uncropped land had no effect on invertebrate biodiversity or ecosystem service provision. Furthermore, landscape compositional and structural complexity only influenced two and four of the 22 ecosystem service and biodiversity response variables measured, respectively. It is likely, given previous findings in Chapter 3, that local factors (*e.g.* margin quality) are stronger drivers of invertebrate biodiversity and ecosystem service provision in arable field margins. Also, it should be noted that these findings were obtained using the focal-patch approach: where the measurements taken within a discrete focal patch (*e.g.* a field margin) are related to the characteristics of the surrounding landscape via statistical procedures (Thornton et al., 2011). Because species composition varies between biotope types (Duflot et al., 2017), a focal-patch approach fails to capture the total invertebrate biodiversity present within a landscape. Therefore, the results presented here only reflect the response of field margin invertebrate communities to landscape complexity and habitat connectivity; other invertebrate communities (*e.g.* woodland invertebrates) may respond differently.

### 5.4.1. Functional habitat connectivity

There are several explanations why functional habitat connectivity failed to affect any of the invertebrate biodiversity and ecosystem service variables measured in this study. Firstly, considering patches of uncropped land as habitat 'islands' and agricultural biotopes as un-crossable patches of non-habitat may have been, in many cases, an oversimplification (e.g. Dennis, 2004, Debinski, 2006, Ewers and Didham, 2006, Dennis et al., 2014). For example, whilst agricultural biotopes may present a largely un-crossable resource-poor barrier to taxa such as butterflies (Dowdeswell et al., 1940, Dover, 1990, Zschokke et al., 2000), many other taxa are readily found dispersing through these areas and accessing the resources within them (Jauker et al., 2012, Garratt et al., 2014b, Orford et al., 2016, Woodcock et al., 2016a). Moreover, most of the invertebrate taxa found within modern agro-ecosystems are generalists capable of withstanding the high disturbance regimes associated with intensive

agriculture (Ekroos et al., 2010, Flohre et al., 2011, Carvalheiro et al., 2013, Gamez-Virues et al., 2015). For such taxa, two patches of uncropped land separated by >25 m of arable land or agricultural grassland may represent a contiguous patch of habitat (*i.e.* areas that provide the necessary resources required to survive *sensu* Dennis, 2012).

A second explanation is that the threshold distance used to determine the functional connectivity between patches of uncropped land was too small and therefore did not accurately reflect how the invertebrates studied perceive the landscape (Tischendorf and Fahring, 2000, Fahrig et al., 2011). The threshold distance was set at 25 m for both practical and ecological reasons. In terms of practicality, setting it below 25 metres resulted in connectance index scores of zero within a high proportion of sample landscapes. Ecologically speaking, a functional connectivity threshold of 25 m encompassed the dispersal capabilities of both low (*e.g.* Carabid beetles) and high (*e.g.* bumblebees and hoverflies) mobility taxa (Coombes and Sotherton, 1986, Holland et al., 2004, Knight et al., 2005, Raymond et al., 2013). However, for high mobility taxa, such as bumblebees and hoverflies, patches of uncropped land separated by much larger distances (*e.g.* 200 metres) are still functionally connected (Knight et al., 2005, Raymond et al., 2013). Indeed, even low mobility taxa, such as certain Carabidae species, may be capable of traversing distances greater than 25 metres over several days (Holland et al., 2004, Holland et al., 2005).

### 5.4.2. Compositional landscape complexity

Landscape management to promote multiple invertebrate biodiversity and ecosystem service benefits is hindered by the fact that individual species/species groups are associated with different biotope types (Carre et al., 2009, Fahrig et al., 2011, Fahrig et al., 2015). Therefore, management prescriptions aimed at enhancing one species group/service may negatively impact upon other species groups/services (i.e. a trade-off sensu Bennett et al., 2009). In the last chapter it was suggested that increasing the compositional complexity of landscapes could resolve this inherent problem. However, this seems unlikely as compositional complexity only affected two of the 22 invertebrate biodiversity and ecosystem service variables measured in this study. In line with previous work (e.g. Bianchi et al., 2006, Gardiner et al., 2009), levels of predation were higher within more compositionally complex landscapes, with Shannon biotope diversity at 1 km having a positive effect on *Calliphora* and *Ephestia* predation. Higher levels of predation are expected in more compositionally complex landscapes because a greater number of biotope types increases the range of available habitat resources, which

should enhance the abundance and diversity of natural enemies (Tscharntke et al., 2005, Bianchi et al., 2006, Chaplin-Kramer et al., 2011). However, natural enemies were unaffected by compositional complexity. One possible explanation for this discrepancy is that only a narrow range of natural enemy taxa predated on the sentinel prey items and these taxa responded positively to compositional complexity. For example, Coccinellidae adults and larvae were the only natural enemy taxa observed feeding on *Ephestia* eggs during the pest control assay, and Gardiner et al. (2009) recorded a positive relationship between landscape compositional complexity and Coccinellidae abundance.

It is generally posited that landscape compositional complexity is an important driver of invertebrate biodiversity and ecosystem service provision within agro-ecosystems (Benton et al., 2003, Tscharntke et al., 2005, Tscharntke et al., 2012b). This view stems from the findings of a multitude of studies purporting to have investigated landscape compositional complexity (e.g. Chaplin-Kramer et al., 2011, Winqvist et al., 2011, Rusch et al., 2013a, Bukovinszky et al., 2017). It therefore seems surprising that most of the invertebrate and ecosystem service response variables measured in this study were unaffected by landscape compositional complexity. Yet, to date, evidence of the positive effect of compositional complexity is scant because the majority of studies have used proxy measurements such as the proportion of arable or uncropped land, rather than quantifying the total diversity of habitats (Fahrig et al., 2011). And where studies have used true measurements of landscape compositional complexity the findings have been mixed (Steckel et al., 2014, Perovic et al., 2015), with some studies suggesting that habitat area is more important (Steffan-Dewenter, 2003, Fuentes-Montemayor et al., 2011). This study also found mixed effects of landscape compositional complexity. Clearly, more studies are required to ascertain the relative importance of landscape compositional complexity on farmland invertebrates and the ecosystem services they provide.

### 5.4.3. Structural landscape complexity

Finally, structural landscape complexity had the greatest effect on the response variables tested. Landscapes containing more complex patch shapes (*i.e.* landscapes with a higher mean shape index) supported greater numbers of aerial and canopy-active natural enemies, and hoverflies. Relatively few studies have investigated the effect of structural landscape complexity on farmland invertebrate populations but results to date seem to suggest that it can have a positive effect on certain taxa (Holzschuh et al., 2010, Kennedy et al., 2013, Steckel

et al., 2014, Fahrig et al., 2015). For example, Holzschuh et al. (2010) found that wasp nest colonisation increased within landscapes containing greater edge densities between biotope types. Similarly, Steckel et al. (2014) found that the abundance and richness of cavity nesting bee and wasp antagonists (predators and parasitoids) was greater within landscapes containing more complex patch shapes. The authors of both studies suggest that the greater number of edge features within structurally complex landscapes may infer a positive effect on certain taxa via facilitating dispersal (Holzschuh et al., 2010, Steckel et al., 2014). This may indeed be the case because several additional studies confirm that groups such as bees, wasps and hoverflies use linear edge features (*e.g.* hedgerows and grass margins) as movement corridors to colonise new habitat or access resources (Holzschuh et al., 2009, Van Geert et al., 2010, Cranmer et al., 2012). In contrast to natural enemies and hoverflies, invertebrate taxonomic richness during transects was negatively affected by increasing structural complexity, which could be due to predation because aerial natural enemies during transects displayed the opposite response, *i.e.* they were found in higher numbers in more compositionally complex landscapes.

### 5.5 Conclusion

The findings of this study indicate that increasing the functional habitat connectivity between patches of uncropped land would have effect on invertebrate biodiversity and ecosystem service provision within arable field margins, since most taxa found on farmland have the capability of dispersing across agricultural fields and/or are adapted to highly disturbed agro-ecosystems. On the other hand, management aimed at increasing compositional complexity at the landscape-scale is likely to enhance pest control services, whereas an increase in structural complexity would benefit aerial and canopy-active natural enemies, and hoverflies by providing a greater proportion of dispersal corridors. However, this may have a negative effect on invertebrate biodiversity by facilitating greater levels of predation.

# Chapter 6: What are the key drivers promoting ecosystem service provision and invertebrate biodiversity within arable field margins?

## 6.1 Introduction

In the coming decades, societal and environmental pressures will place a tremendous burden on agro-ecosystems (Millennium Ecosystem Assessment, 2005, UK National Ecosystem Assessment, 2011, Garibaldi et al., 2017). A growing population will require greater amounts of food, fibre and fuel (*i.e.* provisioning services) (Godfray et al., 2010, Tilman et al., 2011, Miyake et al., 2012), which, even if wastage is reduced, means that agricultural production must rise by 50% in the next thirty years (Baulcombe et al., 2009). However, by degrading biodiversity, the environment and crucial ecosystem services, modern intensive farming methods may undermine the ability of agriculture to support future production demands (Tilman et al., 2002, Foley et al., 2005, Foley et al., 2011, Tilman and Clark, 2015). We are therefore faced with the difficult challenge of creating sustainable agro-ecosystems that deliver multiple ecosystem services simultaneously, whilst protecting farmland biodiversity and mitigating environmental damage (Bommarco et al., 2013, Firbank et al., 2013, Garnett et al., 2013). This will not be easy, especially given our limited understanding of the key drivers that facilitate multiple ecosystem service provision (Kremen and Ostfeld, 2005, Carpenter et al., 2009, Tscharntke et al., 2012a, Bennett et al., 2015), and the paucity of knowledge about how to minimise trade-offs between antagonistic ecosystem services (Bennett et al., 2009).

Despite our general lack of understanding, we do know from experiments and field studies that greater levels of ecosystem multi-functionality (*i.e.* the provision of multiple ecosystem services) are found within biotopes that support a higher species richness of plants (e.g. Cardinale et al., 2012, Tilman et al., 2014, Hautier et al., 2017). In the context of agro-ecosystems, there is strong evidence that management interventions which increase plant diversity deliver additional benefits such as increases in crop yield (via increases in pollination and pest control services), farmland biodiversity, soil fertility (carbon, nitrogen organic matter), and flood alleviation (e.g. Cong et al., 2014, Fischer et al., 2015, Orford et al., 2016, Tschumi et al., 2016a, Isbell et al., 2017, Sutter et al., 2017b). One such management intervention utilised in temperate agro-ecosystems is the creation of arable field margins sown with a diverse mixture of native forb species (Haaland et al., 2011, Holland et al., 2015). These 'forb-rich' field margins are financially subsidised within the European Union under agri-environmental policy (Scheper et al., 2013, Scheper et al., 2015). Individual studies suggest that, in comparison to general grass margins and/or crop fields, forb-rich field margins increase the abundance and richness of flower-visiting insects (including crop pollinators and natural enemies), as well as the pollination and pest control services delivered to the adjacent crop (Haaland et al., 2011, Blaauw and Isaacs, 2014a, 2015, Woodcock et al., 2016a). But to

date, few studies have assessed whether forb-rich field margins can enhance these benefits simultaneously (but see Sutter et al., 2017a), and there are no studies that have investigated the potential additional benefits they may provide, such as climate change mitigation (*e.g.* via soil carbon storage), soil nutrient improvement (*e.g.* via the addition of Fabaceae spp.) and flood alleviation (*e.g.* via improvements to soil infiltration). Nor has there been much attention paid to the attractiveness of forb-rich field margins to agronomically important crop pests (but see Frank, 1998, Eggenschwiler et al., 2013, Grass et al., 2016). Therefore, it is unclear whether the creation of forb-rich field margins will promote ecosystem multifunctionality or if their implementation will result in significant trade-offs between services (*e.g.* local enhancement of both crop pollinators and crop pests) (sensu Bennett et al., 2009). The urgent need to maximise provisioning services means that any land removed from production must be optimised to provide multiple agronomic and biodiversity benefits (Holland et al., 2017b), but this requires a detailed understanding of the management interventions that minimize trade-offs and enhance synergies between ecosystem services flowing from uncropped land (Bennett et al., 2009, Power, 2010).

Whilst forb-rich field margins have the potential to perform many important ecological functions, their ability to do so is likely to be contingent on a range of additional landscape and local factors (see, for example Woodcock et al., 2007b, Rundlöf et al., 2008a, Potts et al., 2009, Sutter et al., 2017a). This is highlighted, for example, by a series of studies which suggest that to maximise the benefit to flower-visitors, flower margins should be implemented in simplified (1–20% uncropped land) rather than complex (>20% uncropped land ) landscapes, since, in the latter case there is enough habitat available that an additional field margin is unlikely to make much difference or provide enough of an 'ecological contrast' to attract insect pollinators (Haenke et al., 2009, Kleijn et al., 2011, Scheper et al., 2013, Scheper et al., 2015). At the local level, field margin management such as cutting frequency, or biotic conditions such as vegetation height and the amount of floral resources in the adjacent hedgerow may also affect the richness and abundance of flower-visitors utilising field margin habitats (Sjodin et al., 2008, Potts et al., 2009, Garratt et al., 2017), which could, in turn, influence the levels of pollination and pest control delivered to the adjacent crop (Blaauw and Isaacs, 2014a, 2015, Woodcock et al., 2016a). Local management and biotic conditions will also regulate the extent to which forb-rich margins provide additional services, including soil carbon storage and soil infiltration. For example, if field margins receive a high volume of farm vehicle traffic, then their capacity to reduce run-off via soil infiltration is likely to be inhibited because of soil compaction (Chyba et al., 2014, Chyba et al., 2017).

Furthermore, field margins that are cut infrequently are likely to have greater soil carbon concentrations than margins with regular cutting regimes (Wang et al., 2011).

The ecosystem multifunctionality of field margins is influenced by both local conditions and the surrounding landscape. The first objective of this chapter is to synthesise the findings of previous chapters by determining the principle factors regulating ecosystem service provision, the abundance of invertebrate ecosystem service providers and the amount of invertebrate biodiversity supported by arable field margins. The factors investigated herein include margin quality (examined in chapter 3), landscape composition (examined in chapter 4), landscape complexity (examined in chapter 5), habitat connectivity (examined in chapter 5) and a range of additional local biotic/abiotic/management variables which have yet to be examined in any previous chapter. As a second objective, and to build on the findings of objective 1, this chapter also aimed to establish the most important individual vegetative components of margin quality for promoting ecosystem multifunctionality, such as forb richness, total forb cover and the cover of several important flower families. The findings of this study will provide farmers with essential information on how to manage arable field margins for multiple ecosystem service benefits.

### 6.2 Data Analysis

Methodological details can be found in Chapter 2. All statistical analyses carried out in this chapter were performed using R v3.2.2 (R Development Core Team, 2016) and the 'lme4' package for linear and generalised mixed-effect models (LMMs and GLMMs, respectively) (Bates et al., 2015). LMMs and GLMMs were validated by visually inspecting residual plots and Shapiro-Wilk tests to check the distribution of residuals, homogeneity of variance and model mis-specification (Zuur et al., 2009, Crawley, 2012). Due to the large number of models run, for brevity, error structures and data transformations for the individual LMMs and GLMMs used in this chapter can be found in Table A8 within the Appendix.

#### 6.2.1. Objective 1: To determine the principle factors regulating ecosystem service provision, the abundance of invertebrate ecosystem service providers and the amount of invertebrate biodiversity supported by arable field margins

This research objective was achieved by exploring how a range of management, abiotic, biotic and landscape predictor variables affected a subset of the invertebrate biodiversity and

ecosystem service response metrics that have previously been examined in Chapters 3 to 5 (Table 6.1). The response variables chosen were those deemed to be the most agronomically important, ecologically relevant and beneficial to wider society. For example, pest control and pollination metrics were chosen because of their importance to farm production (e.g. Ostman et al., 2003, Bommarco et al., 2012). Soil $K_{fs}$ and soil organic matter content were selected due to their role in alleviating the detrimental effects of global environmental change on society, such as flood alleviation (via increases in Soil $K_{fs}$) and atmospheric carbon sequestration (via increases in soil organic matter) (e.g. Stockmann et al., 2013, Lunka and Patil, 2016). For invertebrate ecosystem service providers, canopy-active natural enemies and crop pests recorded during sweep net sampling were selected over epigeal and aerial natural enemies and crop pests because the former are more relevant for natural pest control within arable systems in the UK (Holland et al., 2008, Holland et al., 2012, AHDB, 2014). Canopy-active natural enemies and crop pests were also recorded during the same period as the sentinel prey experiments.

In terms of invertebrate biodiversity, the abundance and richness of Lepidoptera, bumblebees and hoverflies were selected because they are the most ecologically and agronomically relevant invertebrate groups measured in this study. Firstly, day-flying Lepidoptera are a useful bioindicator group for most terrestrial insects apart from saproxylic species (Thomas, 2005). Therefore, if Lepidoptera respond positively to margin quality then it is likely that many other insect taxa will also benefit from forb-rich field margins. Secondly, bumblebees are extremely important pollinators of crops and wild flowers (Goulson et al., 2008, Rader et al., 2016). Thirdly, hoverflies are less efficient, but still important, pollinators of crops and wild species (Jauker and Wolters, 2008, Rotheray and Gilbert, 2011, Jauker et al., 2012), and the larvae of many species also predate on cereal aphids (Sommaggio, 1999). Furthermore, Lepidoptera and bumblebee species have declined dramatically during the last sixty years within the UK, largely due the negative effects associated with intensive farming methods (Goulson et al., 2006, Goulson et al., 2008, Fox, 2013, Fox et al., 2015). And so, establishing mitigation measures for these groups is extremely important for their continual persistence within agro-ecosystems.

The predictor variables used to achieve research objective one are listed in Table 6.2 below. It is important to note that the predictor variables used depended on the response variable being tested (Table 6.2). For example, margin soil type was only entered in soil organic matter and soil $K_{fs}$ models, but margin quality was entered into every model tested (Table 6.2).

**Table 6.1.** (a) Pest control, (b) pollination, (c) soil ecosystem service, (d) invertebrate ecosystem service provider and (e) invertebrate biodiversity response metrics used to achieve research objective 1. The table also shows how and where each variable was measured.

| Response variables | Survey | Measurement location |
|---|---|---|
| *a) Pest control* | | |
| *Calliphora* predation index | Field assay | Crop edge and crop interior |
| *Ephestia* predation index | Field assay | Crop edge and crop interior |
| *b) Pollination* | | |
| No. of fertilised achenes | Field assay | Crop edge and crop interior |
| No. of fruits | Field assay | Crop edge and crop interior |
| *c) Soil services* | | |
| Mean soil $K_{fs}$ | Field measurement | Margin |
| Mean soil organic matter content | Soil sample | Margin |
| *d) Invertebrate ecosystem service providers* | | |
| Crop pollinator abundance | Transects | Margin |
| Canopy-active natural enemy abundance | Sweep netting | Margin, crop edge and crop interior |
| Canopy-active crop pest abundance | Sweep netting | Margin, crop edge and crop interior |
| *e) Invertebrate biodiversity* | | |
| Lepidoptera abundance | Transects | Margin |
| Lepidoptera richness | Transects | Margin |
| Bumblebee abundance | Transects | Margin |
| Bumblebee richness | Transects | Margin |
| Hoverfly abundance | Transects | Margin |
| Hoverfly richness | Transects | Margin |

For each response variable, relevant predictors were entered into LMMs or GLMMs as fixed effects, with site as a random effect. Owing to the large number of predictors, variables were only included within initial models if they had $R^2$ values >0.05. This procedure was carried out to avoid overfitting. Collinearity between predictor variables within initial models was determined by using variance inflation factor and Pearson correlation coefficient thresholds of <3 and <0.65, respectively (Zuur et al., 2009, Zuur et al., 2010). Where predictor variables exceeded this threshold, the predictor with the lowest $R^2$ value was rejected (correlation matrices for this objective were not included in the appendices as the large number of predictors meant the table was too large) (Zuur et al., 2010). Models were simplified by using a backward-stepwise deletion procedure from the starting model (chi-square likelihood ratio tests and ANOVA) until only significant predictors ($P < 0.05$) remained (Zuur et al., 2009,

Crawley, 2012). Before removing a non-significant predictor, models were compared using an ANOVA for a significant increase in residual deviance. If the removal of a non-significant predictor significantly increased the residual deviance, it was returned to the model (Zuur et al., 2009, Crawley, 2012).

**Table 6.2.** The a) management, b) abiotic, c) biotic, d) landscape and e) interaction predictor variables used to achieve research objective 1. The table also shows the response data each predictor variable relates to.

| Predictor variables | Scale/units | Relevant response data[1] |
|---|---|---|
| *a) Management variables* | | |
| Margin seed mixture | grass mix; natural regeneration; flower mix | All |
| Margin cutting frequency | No. of cuts per year | All |
| Margin cuttings | left; removed | All |
| Crop sowing date | winter; spring | Pol, Pest, Trn, Swp |
| *b) Abiotic variables* | | |
| Margin soil type | silt loam; clay loam; sandy loam | *Kfs*, Om |
| Margin vehicle traffic | none; light; intermediate; heavy | *Kfs* |
| Margin bare ground | % | Pol, Pest, Trn, Swp |
| Margin width | metres | Pol, Pest, Trn, Swp, *Kfs*, Om |
| Transect survey season | early; late | Trn |
| Crop position | crop edge; crop interior | Pol, Pest |
| Sweep net position | margin; crop edge; crop interior | Swp |
| *c) Biotic variables* | | |
| Margin quality | low; high | Pol, Pest, Trn, Swp, *Kfs*, Om |
| Margin vegetation height | centimetres | Pol, Pest, Trn, Swp |
| Length of adjacent hedge in flower | metres | Pol, Pest, Trn, Swp |
| Crop weediness | few to none, 1; frequent, 2; abundant, 3 | Pol, Pest, Swp |
| *d) Landscape variables* | | |
| Uncropped land cover | % within 1 km, 500 m & 250 m radii | Pol, Pest, Trn, Swp |
| Arable land cover | % within 1 km, 500 m & 250 m radii | Pol, Pest, Trn, Swp |
| Agricultural grassland cover | % within 1 km, 500 m & 250 m radii | Pol, Pest, Trn, Swp |
| Urban cover | % within 1 km, 500 m & 250 m radii | Pol, Pest, Trn, Swp |
| Shannon biotope diversity index | within 1 km, 500 m & 250 m radii | Pol, Pest, Trn, Swp |
| Shape index | within 1 km, 500 m & 250 m radii | Pol, Pest, Trn, Swp |
| Uncropped connectance index | within 1 km, 500 m & 250 m radii | Pol, Pest, Trn, Swp |
| *e) Interaction terms* | | |
| Margin quality x Crop position | NA | Pol, Pest |
| Margin quality x Transect survey season | NA | Trn |
| Margin quality x Sweep net position | NA | Swp |

[1] All, all data collected; Pol, pollination data; Pest, pest control data; Trn, transect data; Swp, sweep net data; *Kfs*, soil infiltration data; Om, soil organic matter data.

### 6.2.3. Objective 2: To establish the most important vegetative components of margin quality for promoting ecosystem multifunctionality within arable field margins

This research objective was achieved by testing the effect of several forb-based predictor variables on the ecosystem service and invertebrate biodiversity that were significantly influenced by margin quality during research objective one. However, data for response metrics measured at different locations (*e.g.* sweep net, pest control and pollination data) or during different seasons (*e.g.* transect data) was pooled prior to analysis. This was done to establish the overall effect of forb-based predictor variables on the selected response metrics. The forb community predictor variables used included forb richness, total forb cover (%), Fabaceae cover (%), Asteraceae cover (%), Apiaceae cover (%) and 'other' forb cover (%). The other forb category included all flower species that were not Fabaceae, Asteraceae or Apiaceae. These predictor variables are averages of the data collected during vegetation surveys conducted in 2014 and 2016 that was used to construct the quality index scores for each margin plot (§2.2). Apart from Apiaceae cover, all forb-based predictor variables were significantly greater within high quality field margin plots (§2.2). Fabaceae, Asteraceae and Apiaceae were selected as important aspects of the forb community to investigate due to their importance as forage plants for flower-visiting insect taxa, such as bumblebees (*e.g.* Fabaceae and Asteraceae), solitary bees (*e.g.* Asteraceae and Apiaceae), butterflies (*e.g.* Fabaceae and Asteraceae) and hoverflies (*e.g.* Apiaceae and Asteraceae) (Campbell et al., 2012, Dennis, 2012, Wood et al., 2015c, Wood et al., 2016).

The statistical approach used here is largely identical to that used during research objective one. Thus, for each response variable, forb-based predictors were entered into LMMs or GLMMs as fixed effects, with site as a random effect. All forb-based predictors were entered into starting models before determining collinearity using variance inflation factor and Pearson correlation coefficient thresholds of <3 and <0.65, respectively (Zuur et al., 2009, Zuur et al., 2010). Where predictor variables exceeded this threshold, the predictor with the lowest $R^2$ value was rejected (Zuur et al., 2010). Models were simplified by using a backward-stepwise deletion procedure from the starting model (chi-square likelihood ratio tests and ANOVA) until only significant predictors ($P < 0.05$) remained (Zuur et al., 2009, Crawley, 2012). Before removing a non-significant predictor, models were compared using an ANOVA for a significant increase in residual deviance. If the removal of a non-significant predictor significantly increased the residual deviance, it was returned to the model (Zuur et al., 2009, Crawley, 2012).

## 6.3 Results

### 6.3.1. Objective 1: To determine the principle factors regulating ecosystem service provision, the abundance of invertebrate ecosystem service providers and the amount of invertebrate biodiversity supported by arable field margins

Overall, margin quality influenced 14 out of the 15 ecosystem service and biodiversity response metrics measured. In each case, response metrics were recorded at significantly higher levels within or adjacent to high quality margins. For the 12 response metrics that were measured at different positions or at different times of the year, nine were significantly affected by seasonal/positional variables (e.g. transect survey season or sweep net survey position). Four response metrics were influenced by landscape composition variables at 1 km, but the direction of the effect differed between biotope and response metric. None of the ecosystem service or biodiversity response metrics were affected by either the functional connectivity of uncropped land or landscape compositional complexity. However, landscape structural complexity at 1 km remained in one final model where it had a positive effect. Furthermore, margin vegetation height was a significant explanatory variable in four out of the 15 ecosystem service and biodiversity response metrics measured, and in each case, it had a positive effect.

#### *6.3.1.1. Ecosystem service provision*

Margin quality was the most important determining factor of the level of pest control, pollination and soil $K_{fs}$, with every metric being recorded at greater levels within or adjacent to high quality margins (Table 6.3; Figure 6.1; Figure 6.2; Figure 6.3). Besides margin quality, the delivery of pest control services was influenced by landscape composition, as the proportion of agricultural grassland at 1 km had significant positive effect on *Calliphora* predation, and the proportion of arable land at 1 km had a significant negative effect on *Ephestia* predation (Table 6.3a; Figure 6.3b, d). Landscape composition also influenced pollination, since the proportion of uncropped land at 1 km had a positive effect on the number of strawberry fruits produced, but this relationship was only marginally significant ($P < 0.1$) (Table 6.3b; Figure 6.2d). Conversely, the length of the adjacent hedge in flower had a significant positive effect on the mean number of fertilised achenes produced (Table 6.3b; Figure 6.2b). In addition to margin quality, soil $k_{fs}$ monotonically increased as the level of farm vehicle traffic increased (Table 6.3c; Figure 6.3b), whilst soil organic matter was unaffected by

margin quality, but it significantly decreased as margin width increased (Table 6.3c; Figure 6.3c).

**Table 6.3.** Results from LMMs and GLMMs analysing the effect of local and landscape factors on (a) pest control, (b) pollination and (c) soil ecosystem service response variables. All predictor variables retained in the minimum model are included and where appropriate the direction of relationship is shown; ***$P$ <0.001, **$P$ <0.01, *$P$ <0.05, '.'$P$ <0.10.

| Response variables | Significant explanatory variables | d.f. | $\chi^2$ | $P$ |
|---|---|---|---|---|
| *a) Pest control* | | | | |
| *Calliphora* predation index | Margin quality | 1 | 26.28 | *** |
| | % Agriculture grassland at 1 km | 1 | 13.45 | *** (+) |
| *Ephestia* predation index | Margin quality | 1 | 23.67 | *** |
| | Arable land % 1 km | 1 | 5.70 | * (-) |
| *b) Pollination* | | | | |
| No. of fertilised achenes | Margin quality | 1 | 27.39 | *** |
| | Metres of hedge in flower | 1 | 8.31 | ** (+) |
| No. of fruits | Margin quality | 1 | 11.66 | *** |
| | % Uncropped land at 1 km | 1 | 3.32 | . (+) |
| *c) Soil services* | | | | |
| Soil $K_{fs}$ | Margin quality | 1 | 47.72 | *** |
| | Vehicle traffic | 3 | 20.24 | *** |
| Soil organic matter | Margin width (m) | 1 | 15.91 | *** (-) |

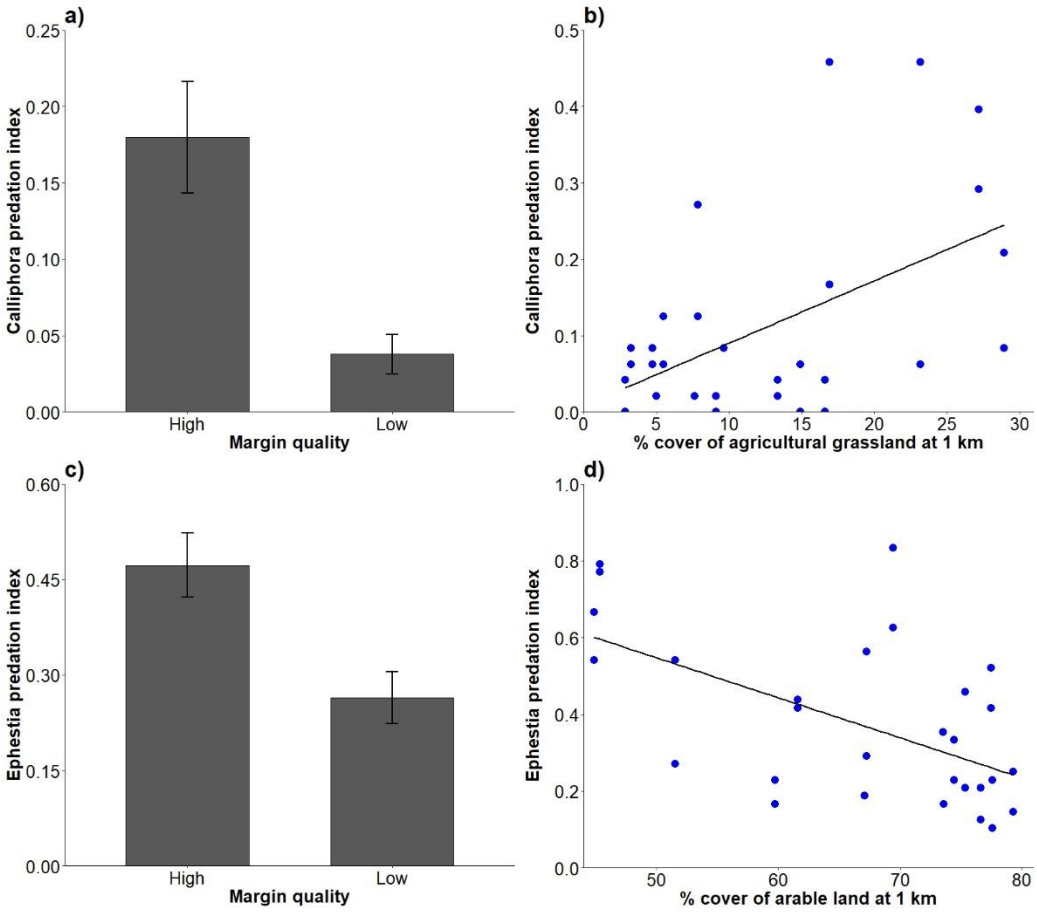


**Figure 6.1.** (a) Mean ± SEM *Calliphora* predation index recorded within cereal crops adjacent to high and low quality margin plots; (b) effect of the % cover of agricultural grassland at 1 km on *Calliphora* predation index; (c) mean ± SEM *Ephestia* predation index recorded within cereal crops adjacent to high and low quality margin plots; and, (d) effect of the % cover of arable land at 1 km on *Ephestia* predation index.

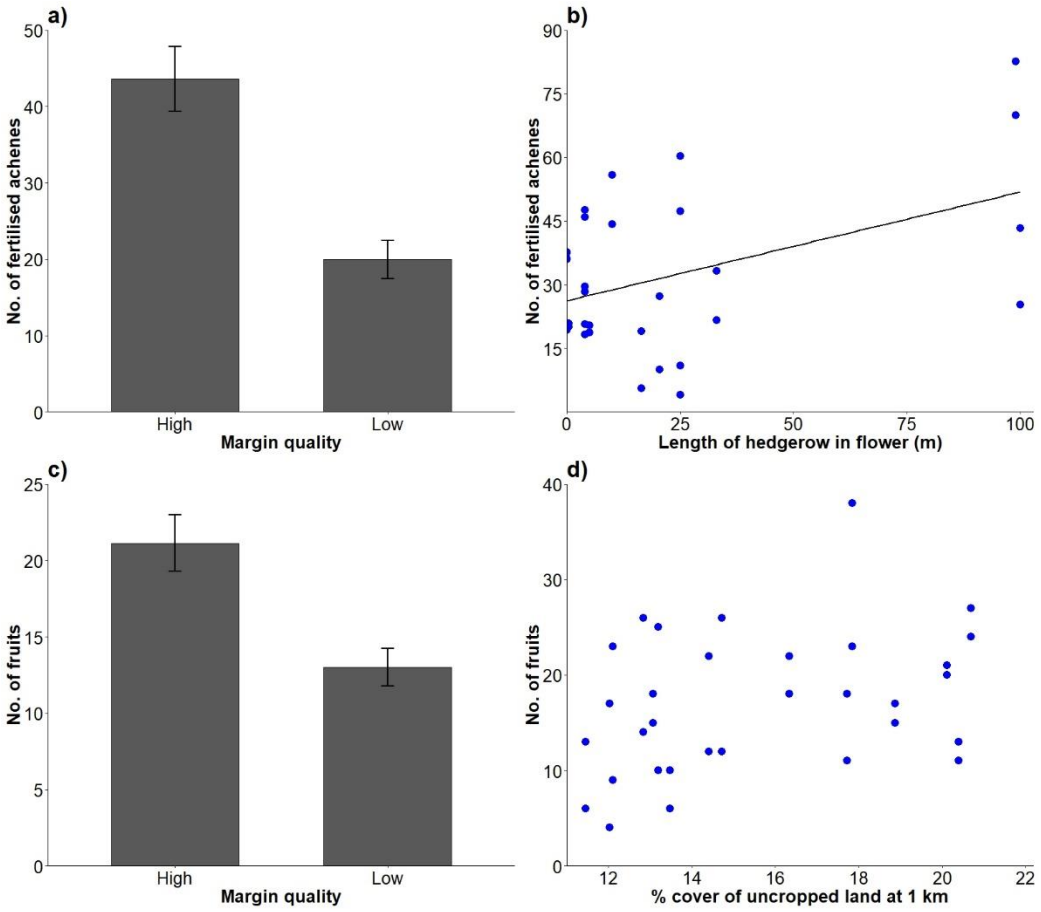


**Figure 6.2.** (a) Mean ± SEM number of fertilised achenes per fruit recorded on strawberry phytometers located within cereal crops adjacent to high and low quality margin plots; (b) effect of length of adjacent hedgerow in flower on the number of fertilised achenes per fruit recorded on strawberry phytometers located within cereal crops adjacent to field margin plots; (c) mean ± SEM number of fruits produced by strawberry phytometers located within cereal crops adjacent to high and low quality margin plots; and, (d) effect of the % cover of uncropped land at 1 km on the number of fruits produced by strawberry phytometers located within cereal crops adjacent to field margin plots.

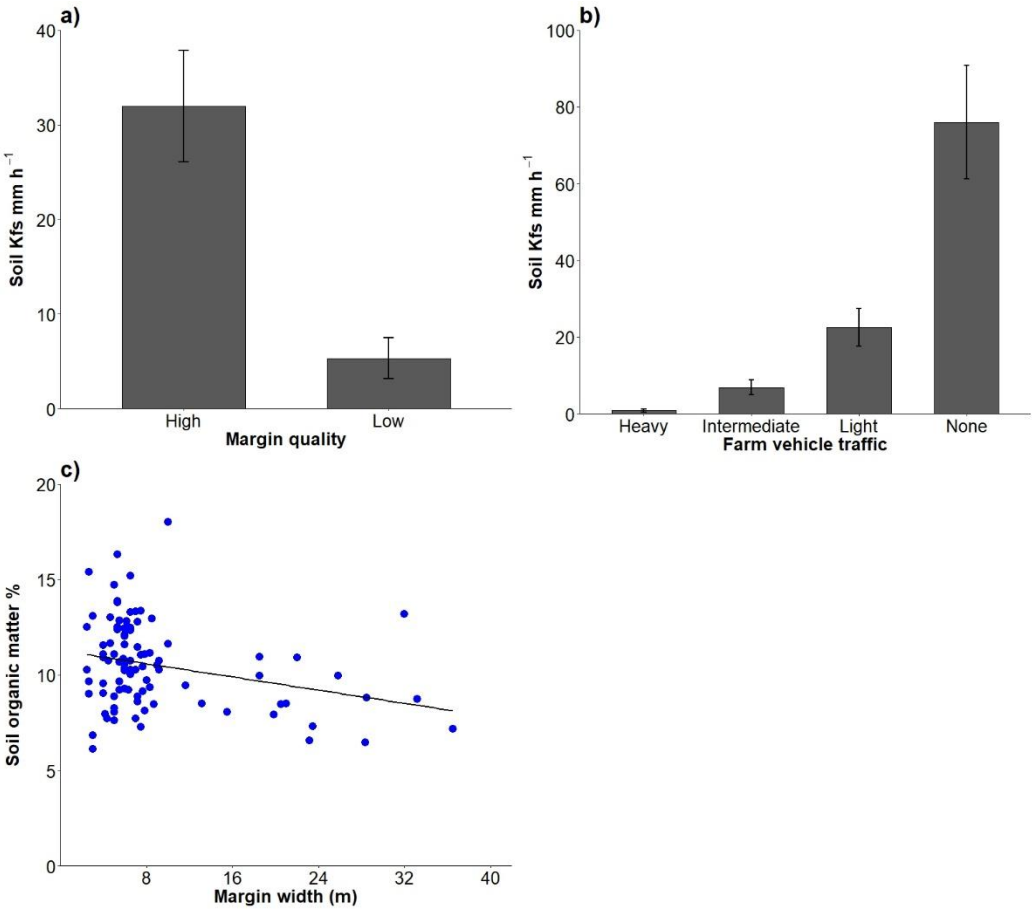


**Figure 6.3.** (a) Mean ± SEM soil $K_{fs}$ (mm $h^{-1}$) values recorded within high and low field margin plots; (b) Mean ± SEM soil $K_{fs}$ (mm $h^{-1}$) values recorded within field margins receiving high, intermediate, light and no levels of farm vehicle traffic; and, (c) effect of field margin width (m) on field margin soil organic matter content (%).

*6.3.1.2. Invertebrate ecosystem service providers*

Transect survey season and margin quality had the greatest effect on crop pollinators, with higher numbers being recorded during the late season and within high quality margins (Table 6.4; Figure 6.4a). The interaction between transect survey season and margin quality also had a marginally significant ($P$ <0.1) effect on crop pollinators, which suggested that the differences in abundance between high and low quality margins were much greater during late season transects (Table 6.4; Figure 6.4a). In addition, the abundance of crop pollinators

recorded during transects significantly increased as margin vegetation height increased (Table 6.4; Figure 6.4b).

**Table 6.4.** Results from LMMs and GLMMs analysing the effect of local and landscape variables on the abundance of crop pollinators recorded during transects, and canopy-active natural enemies and crop pests recorded during sweep net surveys. All predictor variables retained in the minimum model are included and where appropriate the direction of relationship is shown; ***$P$ <0.001, **$P$ <0.01, *$P$ <0.05, '.'$P$ <0.10.

| Response variable | Significant predictor variables | d.f. | $\chi^2$ | $P$ |
|---|---|---|---|---|
| Crop pollinators | Survey season | 1 | 74.5 | *** |
| | Margin quality | 1 | 38.42 | *** |
| | Vegetation height (cm) | 1 | 5.3 | * (+) |
| | Margin quality x Survey season | 3 | 3.35 | . |
| Canopy-active natural enemies | Sweep net position | 2 | 50.55 | *** |
| | Margin quality | 1 | 15.13 | *** |
| | Agriculture grassland % 1 km | 1 | 3.98 | * (-) |
| Canopy-active crop pests | Sweep net position | 2 | 50.55 | *** |
| | Margin quality | 1 | 15.13 | *** |
| | Margin quality x Sweep net position | 5 | 6.48 | * |

During sweep netting, survey position (*i.e.* margin, crop edge, crop interior) and margin quality had the greatest effect on the abundance of canopy-active natural enemies and crop pests, as numbers of both groups monotonically decreased between margin and crop interior sweeps but were always greater within and adjacent to high quality margins (Table 6.4; Figure 6.4c, e). For canopy-active crop pests, the interaction between sweep net position and margin quality remained had a significant effect, since the differences in abundance between high and low quality margins were much greater during margin sweep net samples than during both the crop edge, and crop interior samples (Table 6.4; Figure 6.4e). Also, the proportion of agricultural grassland at 1km had a positive effect on the abundance of canopy-active natural enemies (Table 6.4; Figure 6.4d).

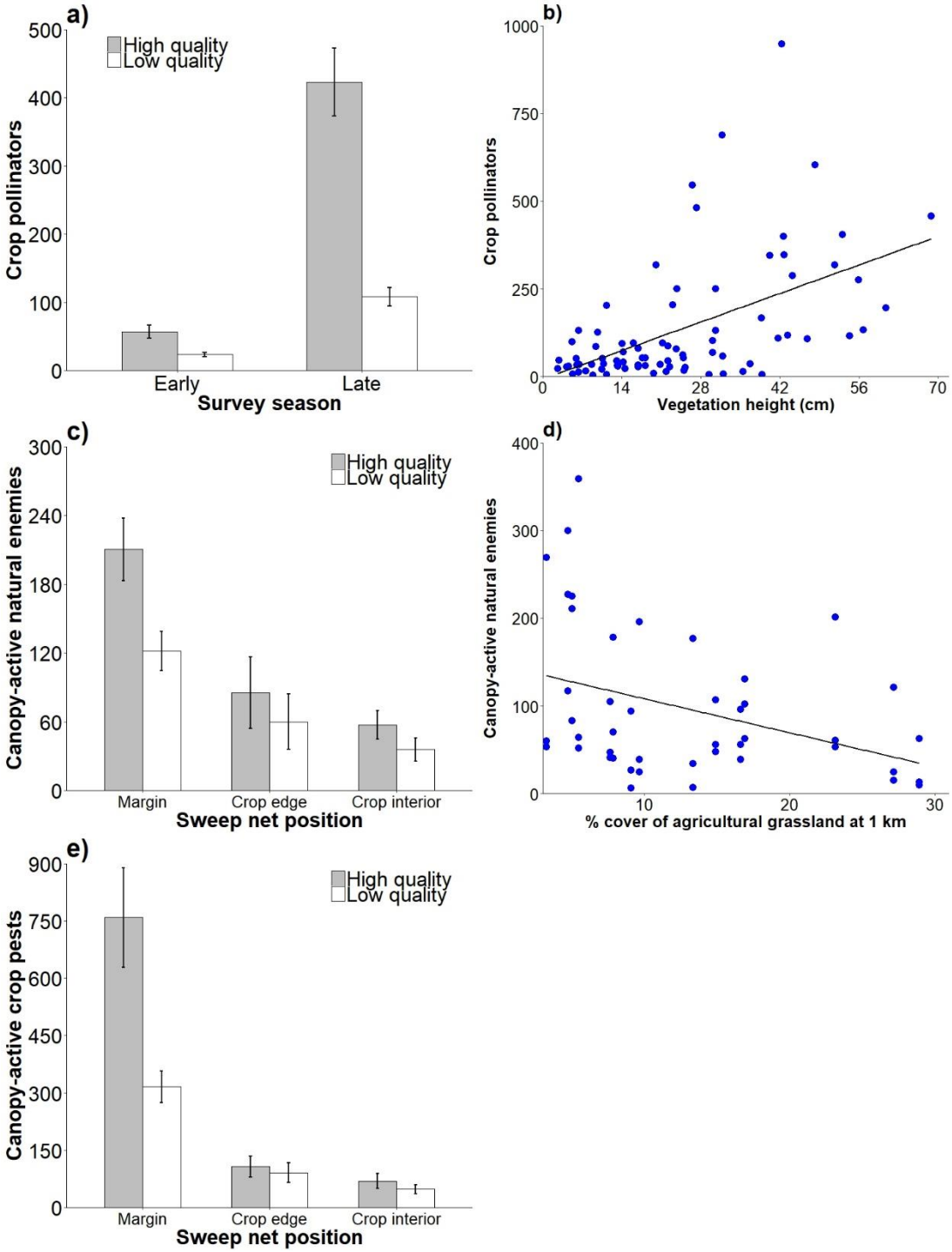


**Figure 6.4.** (a) Mean ± SEM abundance of crop pollinators recorded along transects within high and low field margin plots during different survey seasons; (b) effect of field margin vegetation on the abundance of crop pollinators recorded during transect surveys; (c) Mean ± SEM abundance of canopy-active natural enemies caught within high and low quality margin plots, the crop edge and crop interior during sweep net surveys; (d) effect of % cover of agricultural grassland at 1 km on the abundance of canopy-active natural enemies caught during sweep net surveys; and, (e) Mean ± SEM abundance of canopy-active crop pests caught within high and low quality margin plots, the crop edge and crop interior during sweep net surveys.

*6.3.1.3. Invertebrate biodiversity*

Transect survey season and margin quality had the greatest effect on all six invertebrate biodiversity metrics investigated, with higher values being recorded during the late season and within high quality margins (Table 6.5; Figure 6.5).

**Table 6.5.** Results from LMMs and GLMMs analysing the effect of local and landscape predictor variables on invertebrate biodiversity metrics recorded during transect surveys within field margin plots. All predictor variables retained in the minimum model are included and where appropriate the direction of relationship is shown; ***$P$ <0.001, **$P$ <0.01, *$P$ <0.05, '.'$P$ <0.10.

| Response variable | Significant predictor variables | d.f. | $\chi^2$ | $P$ |
|---|---|---|---|---|
| Lepidoptera abundance | Survey season | 1 | 103.88 | *** |
| | Margin quality | 1 | 29.32 | *** |
| | Margin quality x Survey season | 3 | 5.28 | * |
| Lepidoptera richness | Survey season | 1 | 106.84 | *** |
| | Margin quality | 1 | 27.51 | *** |
| | Margin quality x Survey season | 3 | 5.16 | * |
| Bumblebee abundance | Margin quality | 1 | 123.67 | *** |
| | Survey season | 1 | 122.36 | *** |
| | Margin quality x Survey season | 3 | 58.03 | *** |
| | Vegetation height (cm) | 1 | 17.12 | *** (+) |
| Bumblebee richness | Survey season | 1 | 49.66 | *** |
| | Margin quality | 1 | 19.95 | *** |
| | Vegetation height (cm) | 1 | 7.44 | ** (+) |
| Hoverfly abundance | Survey season | 1 | 78.71 | *** |
| | Margin quality | 1 | 28.12 | *** |
| | Shape index 1 km | 1 | 9.91 | ** (+) |
| | Margin quality x Survey season | 3 | 8.78 | ** |
| Hoverfly richness | Survey season | 1 | 35.83 | *** |
| | Margin quality | 1 | 9.92 | ** |
| | Vegetation height (cm) | 1 | 8.75 | ** (+) |
| | Margin quality x Survey season | 3 | 3.14 | . |

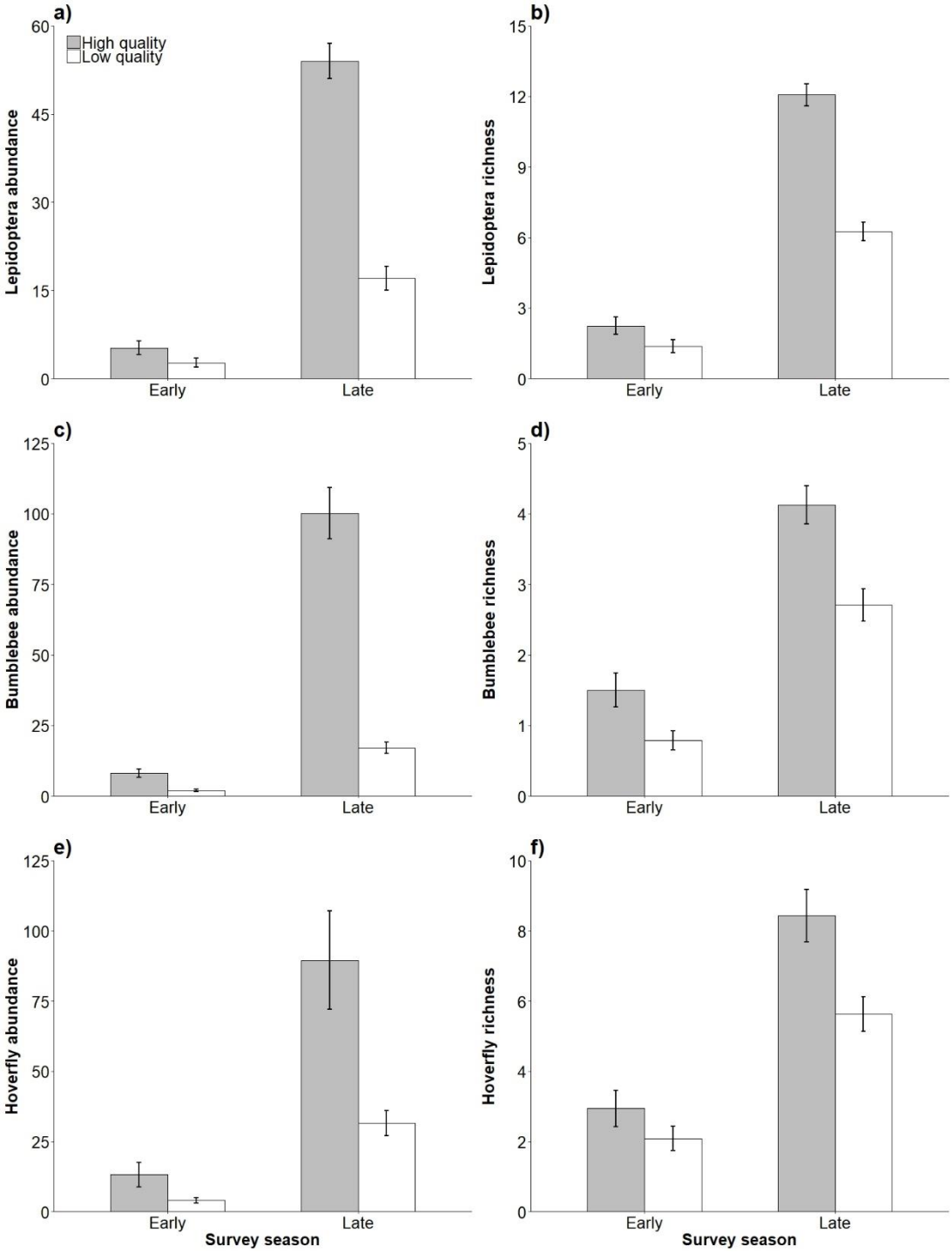


**Figure 6.5.** Mean (± SEM) (a) Lepidoptera abundance, (b) Lepidoptera richness, (c) bumblebee abundance, (d) bumblebee richness, (c) hoverfly abundance and (d) hoverfly richness recorded within high and low quality margin plots during early and late season transect surveys.

The interaction between transect survey season and margin quality also had a significant effect on Lepidoptera abundance and richness, bumblebee abundance, and hoverfly

abundance, as well as a marginally significant effect ($P$ <0.1) on hoverfly richness, since, for all these biodiversity metrics differences between high and low quality margins were much greater during late season transects (Table 6.5; Figure 6.5). In contrast, the interaction between margin quality and survey season was not entered into the model for bumblebee richness. Also, margin vegetation height had a significant positive effect on bumblebee abundance and richness, and hoverfly richness during transect surveys (Table 6.5; Figure 6.6a, b, d), and shape index at 1 km had a significant positive effect on hoverfly abundance (Table 6.5; Figure 6.6c).

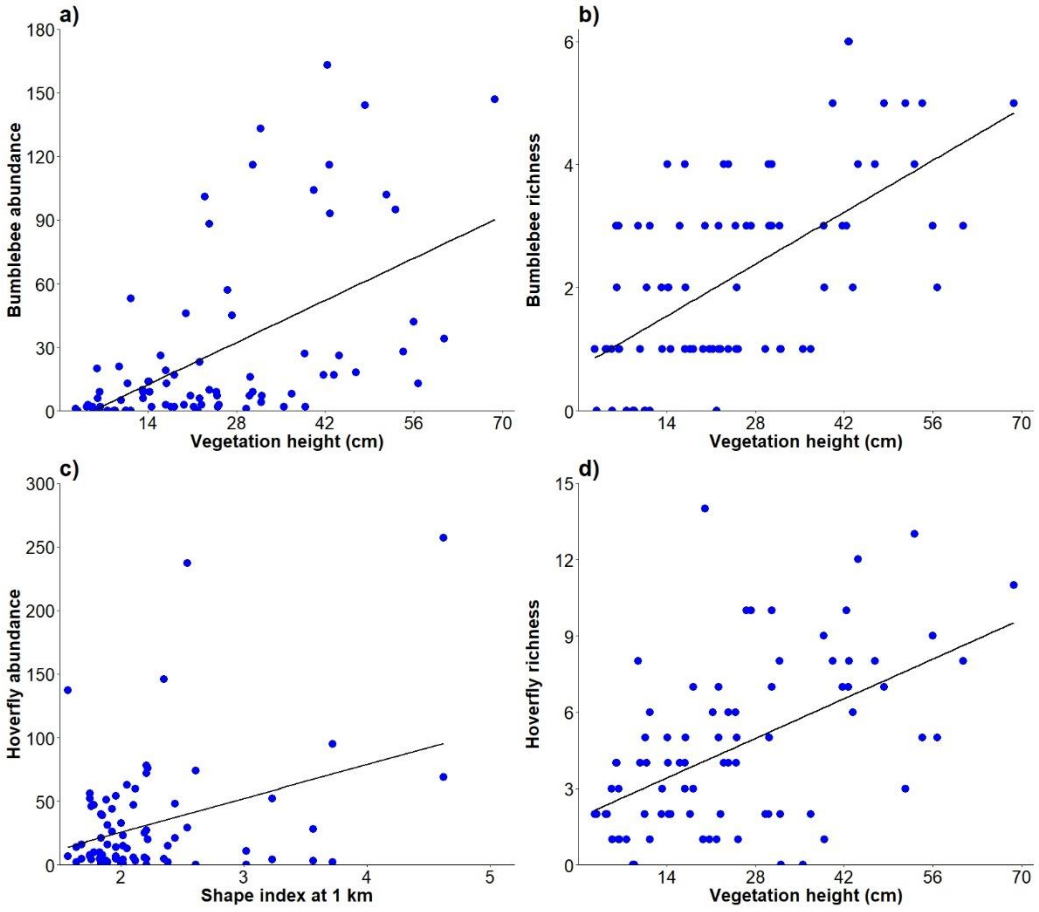


**Figure 6.6.** Effect of field margin vegetation height (cm) on (a) bumblebee abundance and (b) bumblebee richness recorded during transect surveys; (c) effect of shape index at 1 km on hoverfly abundance recorded during transect surveys; and, (d) effect of field margin vegetation height (cm) on hoverfly richness recorded during transect surveys.

### 6.3.2. Objective 2: To establish the most important vegetative components of margin quality for promoting ecosystem multifunctionality within arable field margins

Of the 14 ecosystem service and biodiversity metrics that were significantly affected by margin quality, six were positively affected by the total cover of forbs, five were positively affected by both forb richness and the cover of Asteraceae, three were positively affected by the cover of other forbs (*i.e.* non Asteraceae, Fabaceae or Apiaceae forbs), and one was positively affected by the cover of Fabaceae. The percent cover of Apiaceae had no effect on any ecosystem service and invertebrate biodiversity response metric.

#### *6.3.2.1. Ecosystem service provision*

The percent cover of other forbs had a significant positive effect on *Calliphora* and *Ephestia* predation within the crop adjacent to field margin plots (Table 6.6a; Figure 6.7a, b). Both pollination metrics significantly increased as the percent cover of Asteraceae and forb richness increased within field margin plots (Table 6.6b; Figure 6.7c, d, e). Also, soil $k_{fs}$ significantly increased as the total cover of forbs increased (Table 6.6c; Figure 6.7f).

**Table 6.6.** Results from LMMs and GLMMs analysing the effect of the vegetative components of margin quality on (a) pest control, (b) pollination and (c) soil ecosystem service response variables measured within and adjacent to field margin plots. All predictor variables retained in the minimum model are included and where appropriate the direction of relationship is shown; ***$P$ <0.001, **$P$ <0.01, *$P$ <0.05, '.'$P$ <0.10.

| Response variables | Significant predictor variables | d.f. | $\chi^2$ | $P$ |
|---|---|---|---|---|
| *a) Pest control* | | | | |
| Calliphora predation index | % cover of other forbs | 1 | 6.13 | * (+) |
| Ephestia predation index | % cover of other forbs | 1 | 4.58 | * (+) |
| *b) Pollination* | | | | |
| No. of fertilised achenes | Forb richness | 1 | 8.3 | ** (+) |
| | % cover of Asteraceae | 1 | 4.72 | * (+) |
| No. of fruits | % cover of Asteraceae | 1 | 7.79 | ** (+) |
| | Forb richness | 1 | 7.27 | ** (+) |
| *c) Soil services* | | | | |
| Soil $K_{fs}$ | Total forb cover (%) | 1 | 35.88 | *** (+) |

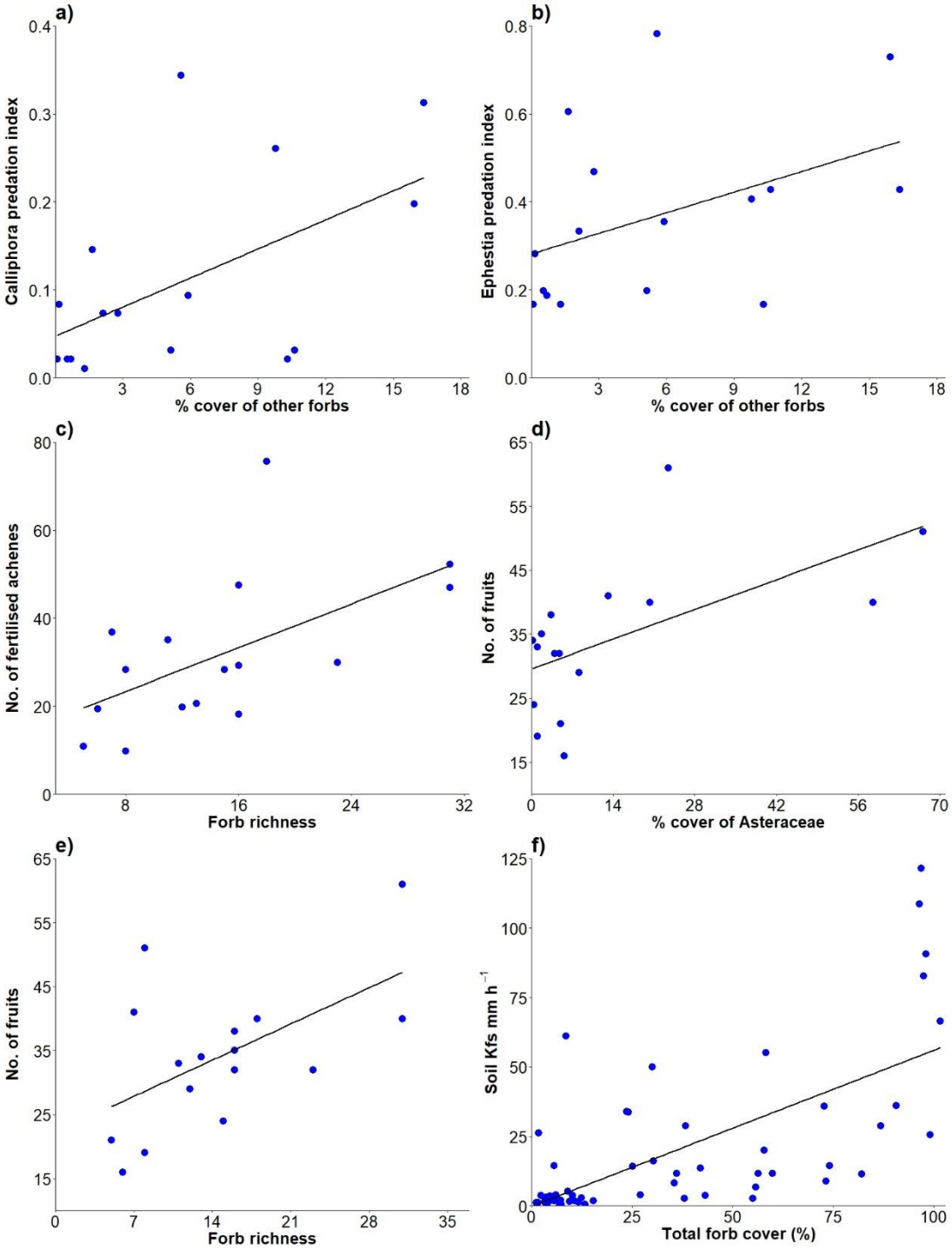


**Figure 6.7.** Effect of % cover of other forbs on (a) *Calliphora* and (b) *Ephestia* predation index; (c) effect of forb richness on the number of fertilised achenes per fruit recorded on strawberry phytometers located within cereal crops adjacent to field margin plots; effect of (d) % cover of Asteraceae and (e) forb richness on the number of fruits produced by strawberry phytometers located within cereal crops adjacent to field margin plots; and, (f) effect of total forb cover (%) on soil $K_{fs}$ (mm $h^{-1}$) values recorded within field margin plots.

*6.3.2.2. Invertebrate ecosystem service providers*

The percent cover of Asteraceae within field margin plots had a significant positive effect on the abundance canopy-active crop pests and a marginally significant positive effect (P <0.1) on the abundance of crop pollinators (Table 6.7; Figure 6.8c). Crop pollinators and canopy-active crop pests were also positively related to total percent cover of forbs and forb richness, respectively (Table 6.7; Figure 6.8a, d). The abundance of canopy-active natural enemies was positively related to the percent cover of Fabaceae within field margin plots (Table 6.7; Figure 6.8b).

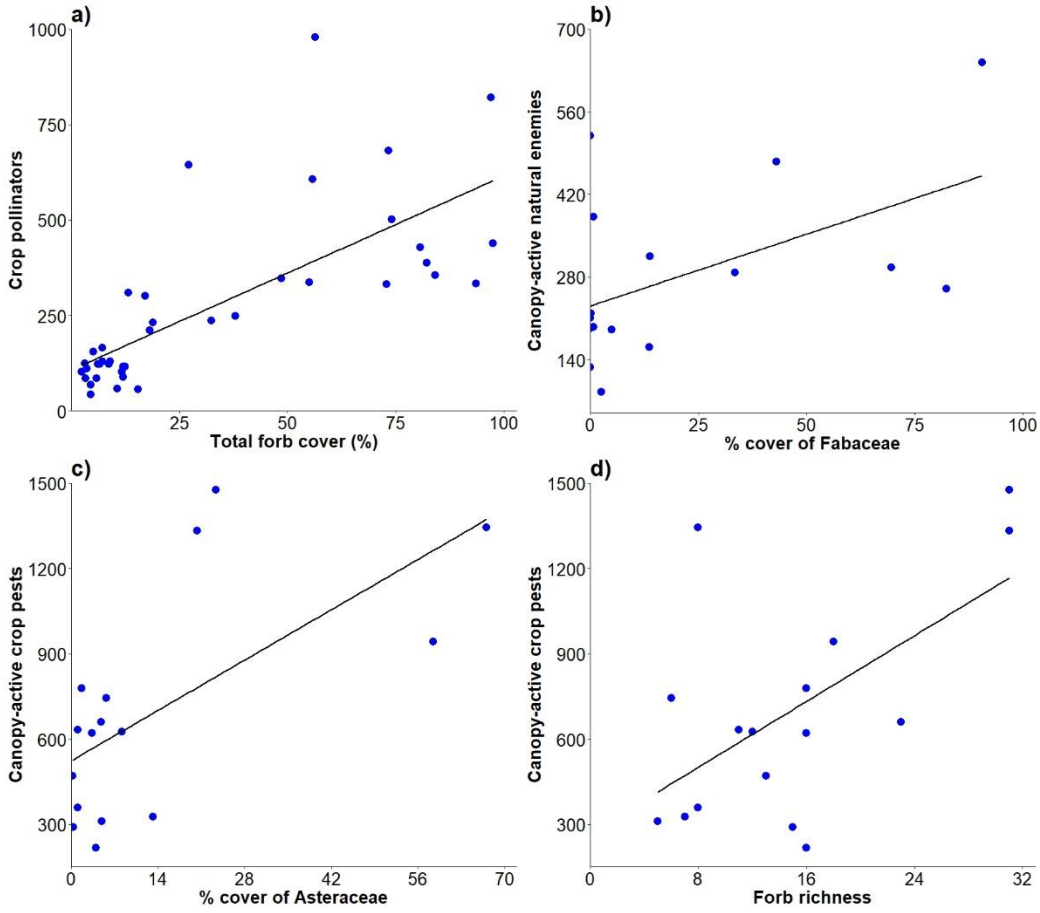


**Figure 6.8.** (a) Effect of total forb cover (%) cover on the abundance of crop pollinators recorded during transects; (b) effect of % cover of Fabaceae on the abundance of canopy-active natural enemies caught during sweep net surveys; (c) effect of % cover of Asteraceae on the abundance of canopy-active crop pests caught during sweep net surveys; and, (d) effect of forb richness on the abundance of canopy-active crop pests caught during sweep net surveys.

**Table 6.7.** Results from LMMs and GLMMs analysing the effect of the vegetative components of margin quality on the abundance of crop pollinators recorded during transects, and canopy-active natural enemies and crop pests recorded during sweep net surveys. All predictor variables retained in the minimum model are included and where appropriate the direction of relationship is shown; ***$P$ <0.001, **$P$ <0.01, *$P$ <0.05, '.'$P$ <0.10.

| Response variable | Significant predictor variables | d.f. | $\chi^2$ | $P$ |
|---|---|---|---|---|
| Crop pollinators | Total forb cover (%) | 1 | 25.88 | *** (+) |
| | % cover of Asteraceae | 1 | 3.65 | . (+) |
| Canopy-active natural enemies | % cover of Fabaceae | 1 | 5.91 | * (+) |
| Canopy-active crop pests | % cover of Asteraceae | 1 | 12.1 | *** (+) |
| | Forb richness | 1 | 9.78 | ** (+) |

*6.3.2.3. Invertebrate biodiversity*

Total forb cover had a highly significant positive effect on Lepidoptera abundance, bumblebee abundance and richness, and hoverfly abundance (Table 6.8; Figure 6.9a, c, d, e). Bumblebee abundance was also positively related to the cover of Asteraceae (Table 6.8). In addition, Lepidoptera richness was positively related to forb richness (Table 6.8; Figure 6.9b), and hoverfly richness was positively related to forb richness and the percent cover of other forbs (Table 6.8; Figure 6.9f).

**Table 6.8.** Results from LMMs and GLMMs analysing the effect of the vegetative components of margin quality on invertebrate biodiversity metrics recorded during transect surveys within field margin plots. All predictor variables retained in the minimum model are included and where appropriate the direction of relationship is shown; ***$P$ <0.001, **$P$ <0.01, *$P$ <0.05, '.'$P$ <0.10.

| Response variable | Significant explanatory variables | d.f. | $\chi^2$ | $P$ |
|---|---|---|---|---|
| Lepidoptera abundance | Total forb cover (%) | 1 | 25.45 | *** (+) |
| Lepidoptera richness | Forb richness | 1 | 39.93 | *** (+) |
| Bumblebee abundance | Total forb cover (%) | 1 | 45.05 | *** (+) |
| | % cover of Asteraceae | 1 | 7.55 | ** (+) |
| Bumblebee richness | Total forb cover (%) | 1 | 16.87 | *** (+) |
| Hoverfly abundance | Total forb cover (%) | 1 | 22.58 | *** (+) |
| Hoverfly richness | Forb richness | 1 | 9.83 | ** (+) |
| | % cover of other forbs | 1 | 4.46 | * (+) |

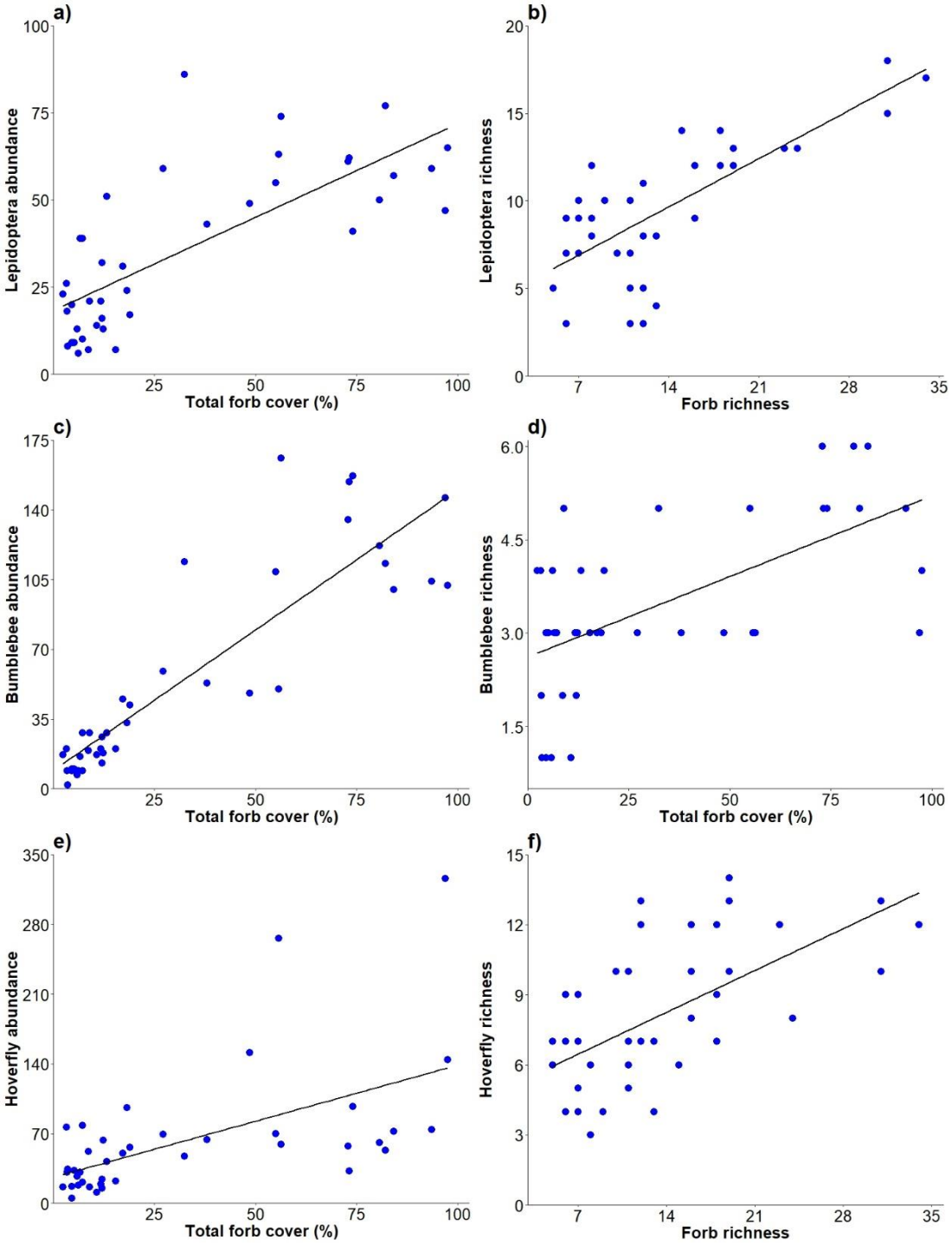


**Figure 6.9.** (a) Effect of total forb cover (%) cover on Lepidoptera abundance recorded during transects; (b) effect of forb richness on Lepidoptera richness recorded during transects; effect of total forb cover (%) cover on (c) bumblebee abundance, (d) bumblebee richness and (e) hoverfly abundance recorded during transects; and, (f) effect of forb richness on hoverfly richness recorded during transects.

### 6.4 Discussion

Agri-environment schemes (AES) were introduced as a mechanism by which farmers could be compensated for taking land out of production or creating habitats for wildlife (Hodge et al., 2015). From 2007 to 2013, €375 million/year was spent on AES in England alone (European Network for Rural Development, 2014). This is a substantial amount money, especially when one considers that the UK governments nature conservation agency, Natural England, spent €250 million on the protection habitats and species between 2013-2014 (Natural England, 2014). It could also be argued that the €375 million/year sum is an inefficient use of taxpayer money given that the efficacy of many AES in delivering tangible benefits for farmland biodiversity is disputed (Kleijn and Sutherland, 2003, Kleijn et al., 2006, Kleijn et al., 2011, but for positive effects see Carvell et al., 2015, Wood et al., 2015c). To justify the relatively large expenditure on agri-environmental management, individual AES options not only need to deliver demonstrable benefits to farmland biodiversity, but they should also promote a suite of additional agronomic and environmental benefits (*i.e.* ecosystem multifunctionality) (Whittingham, 2011, Ekroos et al., 2014, Batary et al., 2015). Moreover, if an AES option was proven to enhance production via increases in services such as natural pest control and pollination, its uptake by farmers and land owners is likely to increase (Bommarco et al., 2013, McKenzie et al., 2013). However, there is currently a paucity of information regarding whether higher levels of ecosystem multifunctionality can be achieved from individual AES options (Ekroos et al., 2014, Batary et al., 2015). Also, apart from the positive effect of increased plant species richness (Isbell et al., 2017), we know little about the factors regulating ecosystem service provision and biodiversity within uncropped land.

This study highlights that higher levels of ecosystem multifunctionality can be promoted in arable field margins by increasing the abundance and richness of forbs. When all potential predictors of ecosystem multifunctionality were considered, high quality margins significantly increased the provision of 14 out of the 15 ecosystem service and biodiversity response metrics measured. For the 14 response metrics influenced by margin quality, forb richness, the total cover of forbs and the cover of Asteraceae were important factors. There was also a consistent positive effect of margin vegetation height on invertebrate biodiversity (hoverfly richness and bumblebee richness and abundance) and ecosystem service providers (crop pollinators). Furthermore, margins receiving less farm vehicle traffic have much greater flood alleviation potential via increases in soil infiltration capacity. Thus, arable field margin management that establishes a high cover and diversity of forbs (particularly Asteraceae spp.),

encourages taller vegetation to develop, and limits the amount of vehicle traffic will deliver multiple invertebrate biodiversity and ecosystem service benefits.

### 6.4.1. Objective 1: To determine the principle factors regulating ecosystem service provision, the abundance of invertebrate ecosystem service providers and the amount of invertebrate biodiversity supported by arable field margins

*6.4.1.1. The effect of margin quality*

In line with previous work, compared to forb-poor low quality margins, forb-rich high quality margins significantly increased pest control and pollination in the adjacent crop (e.g. Blaauw and Isaacs, 2014a, 2015), the abundance of crop pollinators and natural enemies (e.g. Pywell et al., 2011, Woodcock et al., 2016a), and the abundance and richness of Lepidoptera, bumblebees and hoverflies (e.g. Feber et al., 1996, Meek et al., 2002, Carvell et al., 2007, Haaland et al., 2011). This study also demonstrates that, compared to forb-poor grass dominated margins, forb-rich field margins can enhance agronomically important canopy-active crop pests (AHDB, 2014). Pywell et al. (2011) recorded significantly more invertebrate herbivore species within wildflower margins compared to those sown with a grass only mixture and Eggenschwiler et al. (2013) found that slug activity density was 191% higher in flower margins compared to margins dominated by grasses. However, no study to date has demonstrated that invertebrate crop pests as a group are enhanced by forb-rich field margins. Studies in experimental grasslands and mesocosms have highlighted the positive influence of forb species on soil infiltration capacity (Fischer et al., 2015, Gould et al., 2016). But prior to the findings presented here, the positive effect of increased forb richness and cover on soil infiltration has yet to be recorded within field margins. Furthermore, apart from Sutter et al. (2017a), this is the only study to show that, relative to forb-poor grass margins and/or the crop edge, the creation of forb-rich field margins can enhance multiple ecosystem service and biodiversity benefits simultaneously.

The positive effect of forb-rich margins on the abundance of crop pollinators and canopy-active natural enemies, and Lepidoptera, bumblebee and hoverfly abundance and richness is somewhat expected given that these groups require nectar and pollen as a primary (crop pollinators, Lepidoptera, bumblebees and hoverflies) or secondary (natural enemy taxa such as parasitoid wasps) source of nutrition (Goulson, 2003, Wäckers et al., 2005, Rotheray and Gilbert, 2011, Dennis, 2012). Natural enemies may also be attracted to high quality forb-rich margins due to the presence of greater numbers of prey/hosts (Landis et al., 2000, Pywell

et al., 2011, Gurr et al., 2017). It is likely that by attracting greater numbers of crop pollinators and canopy-active natural enemies compared to low quality field margins, high quality field margins encouraged the spill-over of these groups into the adjacent crop and, by doing so, enhanced pest control and pollination services (Blaauw and Isaacs, 2014a, 2015, Woodcock et al., 2016a). The greater numbers of canopy-active crop pests recorded within and in the crop adjacent to high quality field margins could be due to several reasons. Firstly, high quality margins contained significantly more plant species than low quality field margin plots (see Table 2.2 in §2.2), which increases the potential number of hosts that phytophagous crop pests can exploit and may therefore enhance their populations (i.e. the resource specialization hypothesis, Moreira et al., 2016). Secondly, 67.9% of canopy-active crop pests recorded during sweep net surveys are known frequent or occasional flower-visitors, such as Cephidae spp., Chloropidae spp., Curculionoidea spp., Structural spp., Thysanoptera spp. and Tipulidae spp. (Willmer, 2011, Orford et al., 2016). Consequently, such groups will be attracted to field margins containing a greater abundance and richness of flower species. Whatever the mechanisms driving the positive effect of margin quality on crop pests in this study, the attractiveness of forb-rich field margins to undesirable invertebrate groups requires further investigation because farmers would be unwilling to adopt such schemes if they result in increased crop losses and reduced yields. Moreover, this negative trade-off could potentially be reduced by using flower species that only provide resources for beneficial invertebrates (Lavandero et al., 2006, Wäckers et al., 2007, Winkler et al., 2009, Winkler et al., 2010), but the identity of these species needs to be established.

Grasses, with their fine, fibrous and dense root systems may inhibit soil infiltration by limiting the number of soil macropores (*i.e.* reduced soil porosity), whereas a diverse mixture of forbs, with a variety of different, and larger root structures (*e.g.* tap-roots), may enhance soil infiltration by increasing the size and number of soil macropores (*i.e.* increased soil porosity) (Mytton et al., 1993, Mitchell et al., 1995, Obi, 1999, Gould et al., 2016, Huang et al., 2017). Furthermore, some forb families, such as Fabaceae, may further enhance soil infiltration by increasing Lumbricidae populations, which indirectly improve soil porosity via their burrowing and feeding activity (Fischer et al., 2014, Fischer et al., 2015). These mechanisms possibly explain why high quality margins significantly enhanced soil infiltration rates in relation to low quality margins. Indeed, high quality margins supported a greater richness and cover of forbs, as well as a greater cover of Fabaceae spp. (see Table 2.2 in §2.2).

*6.4.1.2. The effect of other local factors*

Soil organic matter content was the only response metric not to be influenced by margin quality, but it was negatively affected by margin width. To the authors knowledge, there are no mechanisms by which margin width can directly influence soil organic matter. Therefore, the negative effect of margin width must be caused by indirect mechanisms. In general, margins that were wider tended to be managed by the removal of cuttings after mowing (mean ± SEM margin width, cuttings left = 7.51 ± 0.59, cuttings removed = 20.27 ± 3.03). Also, for the margins where accurate age data was available (55 out of 98 margin plots), there was a weak but significant negative correlation between margin age and margin width (Pearson coefficient = -0.344, $P$ <0.05). The removal of cuttings in wider field margins could potentially reduce the amount of litter inputs into the soil which would have a negative effect on soil organic matter (e.g. Lajtha et al., 2014). In addition, younger field margins are likely to have a lower proportion of soil organic matter than older field margins (e.g. McLauchlan et al., 2006).

The amount of farm vehicle traffic within field margin plots was determined using a scale based on the depth of wheel ruts. This predictor variable was only entered into the model for Soil $k_{fs}$ because previous work has highlighted how high levels of vehicle traffic within agricultural grasslands increase soil compaction and thus reduce soil infiltration capacity (Chyba et al., 2014, Chyba et al., 2017). Whilst soil compaction was not directly measured, soil $K_{fs}$ increased monotonically as the level of farm traffic decreased. Even though Natural England advise farmers not to drive on field margin plots if possible (Natural England, 2013b, a), this advice is often difficult to adhere to during crop harvest and field boundary management operations. Field margins may also act as access tracks between fields. As a result, many field margin plots receive a great deal of farm vehicle traffic. Nevertheless, this problem could be mitigated if the width of field margins were extended so that there was enough space to drive down the crop side of the margin during harvesting and the boundary side of the margin during management operations, whilst leaving a central strip that receives no/minimal farm vehicle traffic. Another mitigation method may be to use smaller machinery during boundary management operations to reduce the levels of soil compaction (Hamza and Anderson, 2005). Alternatively, given that it is farmers who implement and manage agri-environmental measures, it may be more effective to consult their opinion about ways to mitigate the levels of farm traffic that field margins receive.

Hedgerow species, such as *Crataegus monogyna* and *Prunus spinosa,* are extremely attractive to bumblebees and solitary bees on farmland, especially given that they flower during spring when there is a paucity of floral resources in other uncropped biotopes (*e.g.*

field margins) (Wood et al., 2015b, Wood et al., 2015c, Wood et al., 2016, Cole et al., 2017). And so, margins adjacent to hedgerows providing a greater abundance of floral resources during May should attract greater numbers of bumblebees and solitary bees, which happen to be important pollinators of strawberry (Dimou et al., 2008, Albano et al., 2009, Rader et al., 2016). This may be why the length of hedgerow in flower adjoining field margin plots had a significant positive effect on the mean number of fertilised achenes produced during the phytometer assay. A study by Morandin and Kremen (2013) supports this hypothesis, as they found that, compared to weed strips at the edges of fields, hedgerows promoted the spill-over of wild bees into the adjacent crop. The findings of Garratt et al. (2017) also indicate that hedgerows act as important source habitats from which flower-visitors, such as hoverflies and wild bees, are able to colonise crop fields. The contribution of flower-visitor taxa to the pollination of spring flowering crops in the UK (e.g. oilseed rape, field bean and apple, see Garratt et al., 2014a, Garratt et al., 2014b), combined with the positive effect of hedgerows on the spill-over of flower-visitors into neighbouring fields (Morandin and Kremen, 2013, Garratt et al., 2017) and the potential benefits of spring flowering hedgerows to crop pollination found in this study, emphasises the agronomic importance of hedgerows within agro-ecosystems.

Increasing vegetation height within field margin plots had a positive influence on the abundance of crop pollinators and hoverflies, and the abundance and richness of bumblebees. The positive effect of vegetation height on hoverfly abundance corresponds with the findings of Sjodin et al. (2008), who found, in a study investigating the effect of grazing intensity on flower-visiting insects, that vegetation height (which was negatively correlated with grazing intensity) had a significant positive effect on hoverfly abundance. They suggested that this relationship is because taller swards constitute a greater biomass, which should provide more prey for hoverfly larvae, *i.e.* taller vegetation is more attractive oviposition habitat for hoverfly species with predatory larvae (*ibid*). This may also explain why hoverfly species richness was not influenced by vegetation height, since many hoverfly species have non-predatory larvae (Rotheray and Gilbert, 2011). In contrast to hoverfly abundance, the positive effect of vegetation height on bumblebee abundance and richness contradicts the findings of Ockinger and Smith (2007), who, in a study within semi-natural grasslands and uncultivated field margins, found that bumble species richness and abundance was unaffected by vegetation height. One possible explanation for this is that vegetation height was positively correlated with the abundance of floral units and number of species in flower recorded during margin transects when bumblebees were surveyed (margin vegetation height *vs* the number of floral

units: Pearson coefficient = 0.395, *P* <0.001; margin vegetation height *vs* the number of species in flower: Pearson coefficient = 0.340, *P* <0.01). The abundance of floral units and number of species in flower were not included within invertebrate biodiversity models because the inclusion of margin quality meant that they were statistically redundant.

Predictably, the abundance of crop pollinators, and the abundance and richness of Lepidoptera, bumblebees and hoverflies were all significantly greater during late season transect surveys. Also, the interaction between margin quality and survey season had a marginally significant positive effect on the abundance of crop pollinators and hoverfly richness, and a significant positive effect on Lepidoptera abundance and richness, and the abundance of hoverflies and bumblebees. This suggests that these response metrics were always recorded at greater levels within high quality margins, but the differences between margin types were much greater during late season transect surveys. These results mirror, and are likely to be explained by, seasonal floral resource provision within field margins plots (see §3.2.2). Moreover, floral resource data also suggests that there is scope to enhance flower-visitors during the early season by encouraging early flowering forb species within field margin plots (see §3.2.2 and 3.3.2). Another predictable finding was the significant decrease of canopy-active crop pests and natural enemies between margin and crop interior sweep net sample locations. This is unsurprising because, in general, field margins provide a wider-range of habitat resources than cereal fields (Landis et al., 2000, Cole et al., 2017, Gurr et al., 2017).

*6.4.1.3. The effect landscape factors on invertebrate ecosystem services and biodiversity*

Landscape factors were relatively unimportant as they only influenced five out of the 15 ecosystem service and biodiversity response metrics examined. Four of these landscape factors were compositional metrics, whereas one was a measure of landscape complexity (shape index). Response metrics largely responded to different landscape predictors, but if the same landscape predictor affected more than one response metric, the relationships were contradictory. However, response metrics consistently responded to landscape factors at 1 km, which suggests that this is the most important scale at which to conduct landscape-level management within agro-ecosystems.

Shape index, which is a measure of landscape structural complexity (Fahrig et al., 2011), had a positive effect on hoverfly abundance. Higher shape index scores reflect more complex patch shapes with a greater proportion of edge to core (McGarigal et al., 2002). Within agricultural landscapes, hoverflies use edge features, such as hedgerows as dispersal

corridors to move between habitat patches (Cranmer et al., 2012). Therefore, landscapes with more complex shapes, like those found in agro-ecosystems with smaller field sizes (Fahrig et al., 2015), are likely to facilitate hoverfly dispersal and thus, elevate numbers utilising resource-rich patches of uncropped land, such as field margin biotopes. Contrary to the results of Chapter 4, the proportion of uncropped land at 1 km only had a marginally significant ($P$ <0.10) positive effect on the mean number of fruits produced during the phytometer assay. It seems that the effect of uncropped land on the number of fruits produced is secondary to local factors, such as margin quality.

The two pest control metrics measured were influenced by different landscape composition metrics: the proportion of arable land at 1 km had a negative effect on *Ephestia* predation, whereas the proportion of agricultural grassland had a positive effect on *Calliphora* predation. The former result is in line with previous findings regarding the negative effect of agricultural intensification (*viz.* landscape simplification) on natural pest control (Rusch et al., 2016b), and the latter result probably reflects the lower levels of disturbance and greater resource provision within agricultural grasslands in comparison to arable fields (Herzog et al., 2006, Werling et al., 2011, Werling et al., 2014, Cole et al., 2017). Counterintuitively, agricultural grassland at 1 km had negative effect on the abundance of canopy-active natural enemies recorded during the same period in which pest control assays were conducted. However, this result does not necessarily suggest that agricultural grasslands have a negative effect on canopy-active natural enemy populations at the landscape-scale. For example, it could be due to dilution (sensu Holzschuh et al., 2011, Holzschuh et al., 2016), whereby canopy-active natural enemies are drawn away from uncropped biotopes in landscapes with a high proportion of agricultural grasslands because the latter provides important habitat resources for many taxa. But this hypothesis could not be verified because the habitat quality of agricultural grasslands was not quantified during landscape data collection. Overall, the landscape effects found here suggest that invertebrate ecosystem services and biodiversity are likely to be better promoted within more mixed agro-ecosystems (arable and livestock), with smaller fields and higher proportions of uncropped land.

### 6.4.2. Objective 2: To establish the most important vegetative components of margin quality for promoting ecosystem multifunctionality within arable field margins

By establishing the most important vegetative components of margin quality, this objective aimed to provide more specific management prescriptions for promoting ecosystem

multifunctionality within arable field margins. However, it also highlighted significant trade-offs between ecosystem services and disservices. Table 6.9 displays the significant relationships between the vegetative components of margin quality and biodiversity/ecosystem service response variables.

**Table 6.9.** A summary table showing the significant relationships recorded between the vegetative components of margin quality and biodiversity/ecosystem service response variables.

| Response variable | Total forb richness | Total forb cover | Asteraceae cover | Fabaceae cover | Other forb cover |
|---|---|---|---|---|---|
| *Calliphora* predation | | | | | + |
| *Ephestia* predation | | | | | + |
| No. of fertilised achenes | + | | + | | |
| No. of fruits produced | + | | + | | |
| Soil $K_{fs}$ | | + | | | |
| Crop pollinators | | + | + | | |
| Canopy-active natural enemies | | | | + | |
| Canopy-active crop pests | + | | + | | |
| Lepidoptera abundance | | + | | | |
| Lepidoptera richness | + | | | | |
| Bumblebee abundance | | + | + | | |
| Bumblebee richness | | + | | | |
| Hoverfly abundance | | + | | | |
| Hoverfly richness | + | | | | + |

In combination, total forb richness (5 metrics), total forb abundance (4 metrics), Asteraceae abundance (4 metrics) and the abundance of other forbs (3 metrics) enhanced 13 of the 14 response metrics significantly affected by margin quality. However, forb richness and the abundance of Asteraceae also enhanced the abundance of crop pests whilst simultaneously benefiting pollination (forb richness and Asteraceae abundance), hoverfly richness (forb richness), Lepidoptera richness (forb richness), bumblebee abundance (Asteraceae abundance) and crop pollinator abundance (Asteraceae abundance). The positive effect of Fabaceae abundance on canopy-active natural enemies is surprising given that, in general, many flower-visiting natural enemy taxa (*e.g.* parasitoid wasps and hoverflies) do not visit species within this family for pollen and nectar (Wäckers, 2004, van Rijn and Wäckers, 2016). The abundance of Fabaceae spp. probably attracted natural enemies because of their role as

hosts for aphid species (Holman, 2009), which also highlights another potential mechanism by which forb-rich field margins may enhance canopy-active crops pests.

### 6.5 Conclusion

In summary, the findings presented in this study suggest that, to promote higher levels of ecosystem multifunctionality within arable field margins, farmers should aim to create wider field margins, which receive a minimal amount of vehicle traffic and contain a high cover and richness of forbs, especially species within Asteraceae and Fabaceae. Management should also aim to promote taller swards and margins should be left in place for as long as possible as this is likely to increase soil carbon sequestration via the accumulation of organic matter over time. In addition, situating margins adjacent to hedgerows that provide an abundant source of pollen and nectar early in the season may promote increased pollination of spring flowering crops such as oilseed rape and field bean. In terms of landscape management, the ability of arable field margins to deliver invertebrate mediated ecosystem services will be enhanced by the creation of smaller crop fields (*e.g.* via hedgerow planting or field margin establishment) and a shift to more mixed farming systems (*i.e.* an increase in agricultural grassland). However, further research is required to determine the mechanisms driving the positive effect of margin quality on crop pests found in this study. Part of this research will involve establishing a suite of flower species that only enhance beneficial invertebrate taxa.

# Chapter 7: Summary of key findings, best practice guidelines for farmers and next steps

### 7.1 Restatement of context and research aims

Agro-ecosystems are essential to human wellbeing because they provide us with food, fibre and fuel (Millennium Ecosystem Assessment, 2005, UK National Ecosystem Assessment, 2011). But the production of these goods is dependent upon a range of ecosystem services mediated by farmland biodiversity, including crop pollination, natural pest control and nutrient cycling (Zhang et al., 2007, Power, 2010, Bommarco et al., 2013). In countries like the UK where agriculture is the dominant land-use (DEFRA, 2016b), agro-ecosystems could also be managed to provide additional societal benefits, such as climate change mitigation and wildlife conservation (Swinton et al., 2007, Wratten et al., 2012, Firbank et al., 2013). However, the ability of agro-ecosystems to produce food and to supply secondary ecosystem service benefits is under threat from two interacting processes: modern intensive farming methods (*e.g.* agrochemical use and enlarged cropping units) and the need to feed an expanding human population (Tilman et al., 2002, Foley et al., 2005, Zhang et al., 2007, Tilman and Clark, 2015). Intensive agriculture is a major cause of biodiversity loss, ecosystem degradation and global environmental change (Foley et al., 2011, Tilman et al., 2011, Phalan et al., 2016). Paradoxically however, these processes are eroding the very ecosystem services that facilitate agricultural production (Diaz et al., 2006, Power, 2010, Tai et al., 2014). Therefore, if we are to succeed in feeding rapidly expanding human population, we need to change the way we farm (Godfray et al., 2010, Tilman et al., 2011, Tilman and Clark, 2015).

One solution is to pursue 'ecological intensification', whereby the elements of biodiversity essential for agricultural production are encouraged in order to maximise yields whilst reducing our reliance on intensive farming methods (*e.g.* agrochemical use) (Bommarco et al., 2013, Harrison et al., 2014, Potts et al., 2015, Garibaldi et al., 2017). In Europe, agri-environment schemes (AES) are currently the principle tool by which farmland biodiversity is protected from the deleterious effects of modern agriculture (Kleijn et al., 2011, Scheper et al., 2013, Ekroos et al., 2014). By doing so, they may also support a range of ecosystem services that facilitate agricultural production and benefit wider society (Whittingham, 2011, McKenzie et al., 2013). Thus, the implementation of AES by farmers may significantly contribute to the ecological intensification of modern agro-ecosystems (Bommarco et al., 2013). One AES option that has the potential to deliver agronomically important ecosystem services is the creation of forb-rich arable field margins (Wratten et al., 2012), which have the principle aim of providing high quality foraging habitat for flower-visiting insects (Scheper et al., 2015, Grass et al., 2016). Not only do forb-rich field margins increase the local abundance and richness of flower-visitors in comparison to forb-poor grass margins and/or crop edges (Haaland et al.,

2011), but, by enhancing natural enemies and pollinating insects, they also increase pollination and natural pest control in the adjacent crop (Blaauw and Isaacs, 2014a, 2015, Woodcock et al., 2016a, Sutter et al., 2017a).

Despite these demonstrable benefits, there are several unknowns regarding the effectiveness of forb-rich field margins in enhancing biodiversity and ecosystem service provision. Firstly, few studies have established if forb-rich field margins can enhance flower-visiting insects, pest control and pollination simultaneously (but see Sutter et al., 2017a). Moreover, since the creation of forb-rich margins removes land from production and increases local plant diversity, they may also provide additional ecosystem services, including carbon sequestration and flood alleviation (Wratten et al., 2012, Cong et al., 2014, Fischer et al., 2015, Isbell et al., 2017). But no study to date has examined the extent to which forb-rich field margins enhance these services. Secondly, in the UK, seed mixes for forb-rich margins were primarily developed by studying bumblebee flower preferences (Kells et al., 2001, Carvell et al., 2004, Pywell et al., 2005b, Carvell et al., 2006, Pywell et al., 2006, Carvell et al., 2007, Pywell et al., 2011). Consequently, they may not be as effective as they could be at enhancing other flower-visiting taxa, including important crop pollinators and natural enemies such as solitary bees and parasitoid wasps (Campbell et al., 2012, Wood et al., 2015b, Wood et al., 2016). But little is known about the value of field margin flower species to the wider flower-visiting community (but see Wood et al., 2016). Thirdly, we also lack data on the attractiveness of forb-rich field margins to agronomically important crop pests (but see Frank, 1998, Eggenschwiler et al., 2013, Grass et al., 2016). Finally, we have an incomplete picture regarding how the composition and complexity of the surrounding landscape, in combination with local abiotic/biotic and management factors, determine ecosystem service provision within agro-ecosystems.

This study addressed these research gaps with the broad objective of providing farmers and land managers with a manual for enhancing ecosystem services and invertebrate biodiversity within arable field margins. As such, the specific aims were:

1. To determine whether high quality forb-rich field margins deliver multiple ecosystem services more effectively than low quality forb-poor field margins (Chapter 3).

2. To investigate whether arable field margins currently provide sufficient foraging resources for flower-visiting insects (Chapter 3).

3. To examine how the proportion of different biotopes at the landscape scale influences invertebrate biodiversity and ecosystem service provision within arable field margins (Chapter 4).

4. To examine how landscape complexity and habitat connectivity influence invertebrate biodiversity and ecosystem service provision within arable field margins (Chapter 5).

5. To establish the key drivers (both local and landscape) promoting ecosystem service provision and invertebrate biodiversity within arable field margins (Chapter 6).

## 7.2 Summary of key findings

### 7.2.1 Chapter 3

Using an index of margin quality based on the cover and richness of forbs, this chapter explored whether: (i) the quality index is valid and reliable measure of flower-visitor foraging habitat; (ii) arable field margins AES arable field margins benefit the wider flower-visiting community (*i.e.* non-bee flower-visitors); (iii) high quality forb-rich field margins promote ecosystem services and biodiversity more effectively than low quality forb-poor field margins; (iv) increasing field margin quality promotes ecological multifunctionality.

#### *7.2.1.1 Validation of quality index*

Transect data revealed that the quality index was an accurate measure of flower-visitor foraging habitat quality because, compared to low quality forb-poor field margins, forb-rich high quality field margins contained more floral resources, and supported greater numbers of honeybees, bumblebees, solitary bees, parasitoid wasps, Lepidoptera, hoverflies, non-Syrphid Diptera and beetles. Furthermore, a greater proportion of flower-visitor taxa were observed feeding within high quality margins. In terms of the flower-visiting community, the results of this chapter, like the findings of Grass et al. (2016), suggest that field margins support a diverse range of flower-visitor taxa. An interesting finding was that beetles and non-syrphid Diptera were the first and second most dominant taxa in both margin types. For beetles, >90% of records were of Nitidulidae spp., which is a family that contains the agronomically damaging pest of oilseed rape *Meligethes aeneus*. Unsurprisingly, bumblebees, solitary bees and

honeybees constituted a larger proportion of the flower-visitor community within high quality margins. However, on their own, solitary bees only comprised <2.3% of the flower-visitor community in both margin types.

*7.2.1.2 Field margin floral resources*

Comparisons of seasonal floral richness and abundance highlighted that field margins are floristically poor during May and early June, which could be addressed by including early flowering species in seed mixes such as *Anthriscus sylvestris*, *Ranunculus repens* and *Taraxacum agg*. Insect flower preferences revealed that forb species not currently included within AES seed mixes were more important and this was the case even for bumblebees, even though AES forb-rich field margins being largely based on bumblebee flower preferences. Despite their importance as forage plants, non-AES forb species comprised only a small proportion of the flower community. However, some of the most attractive non-AES forb species were attractive to crop pests or pernicious weeds.

*7.2.1.3 The effect of margin quality on ecosystem services and invertebrate biodiversity*

Compared to low quality margins, high quality margins: promoted greater levels of pollination and pest control in the adjacent crop; had a greater soil infiltration capacity; supported a greater abundance of crop pollinators, aerial and canopy-active natural enemies and crop pests; supported a greater abundance and richness of bumblebees, day-flying Lepidoptera and hoverflies; and, supported a greater richness of invertebrate taxa. However, margin quality had no effect on soil carbon, nitrogen or organic matter content, nor on the abundance of epigeal natural enemies and crop pests. In general, the richness and abundance of all invertebrate groups measured using transects was greater during late season surveys. Also, the richness and abundance of all invertebrate groups measured during sweep netting decreased monotonically between the margin and crop interior samples.

*7.2.1.4 Increasing field margin quality promotes ecological multifunctionality*

Overall, increasing field margin quality enhanced 17 out of the 24 ecosystem service and biodiversity metrics tested, which provides strong evidence that forb-rich field margins promote ecological multifunctionality. However, the strong positive effect of quality on

canopy-active crop pests is a worrying finding and suggests that forb-rich field margins could potentially have a detrimental effect crop production.

### 7.2.2 Chapter 4

This chapter explored how the proportion of uncropped land, arable land, agricultural grassland and urban land at three spatial scales (1 km, 500 m, 250 m) influenced the provision of pest control and pollination services, and invertebrate biodiversity. Overall, landscape composition metrics influenced eleven out of the 19 invertebrate biodiversity and ecosystem service response variables tested. Individual response variables were largely influenced by different biotope classes at 1 km. This made it difficult to draw any clear conclusions regarding how to manage landscapes to promote invertebrate biodiversity and ecosystem service provision.

### 7.2.3 Chapter 5

In this chapter, we tested the effect of landscape complexity (compositional and structural) and the connectivity between patches of uncropped land at three spatial scales (1 km, 500 m, 250 m) on the provision of pest control and pollination services, and invertebrate biodiversity. The connectivity between patches of uncropped land had no effect on any of the 19 invertebrate biodiversity and ecosystem service response variables tested. Landscape compositional complexity (SHBDI index) at 1 km had a strong positive effect on both *Calliphora* and *Ephestia* predation but had no effect on any of the other response variables. Landscape structural complexity (shape index) had the greatest effect overall, but still only influenced four response metrics. Shape index at 1 km had a positive effect on the abundance of aerial natural enemies and hoverflies, whereas shape index at 500 m had a positive effect on the abundance of canopy-active natural enemies, but a negative effect on the richness of invertebrate taxa recorded during transects.

### 7.2.4 Chapter 6

There were two specific objectives explored in this chapter. Firstly, to determine the principle factors regulating ecosystem service provision, the abundance of invertebrate ecosystem service providers and the amount of invertebrate biodiversity supported by arable field margins. The factors investigated include margin quality, landscape composition, landscape

complexity (compositional and structural), the connectivity between patches of uncropped land and a range of additional local biotic/abiotic/management variables. Secondly, this chapter aimed to establish the most important vegetative components of margin quality for promoting ecosystem multifunctionality, such as forb richness, total forb cover and the cover of several important flower families. The results indicated that the margins which promoted higher levels of the ecosystem service and invertebrate biodiversity were those that: contained a high cover and richness of forbs, especially species within Asteraceae and Fabaceae; received a minimal amount of vehicle traffic; had taller swards; and, were situated next to hedgerows providing abundant floral resources in spring.

In addition, leaving margins in place for longer is likely to increase soil carbon sequestration via the accumulation of organic matter over time. Regarding landscape management, the creation of smaller crop fields (*e.g.* via hedgerow planting or field margin establishment) and a shift to more mixed farming systems (*i.e.* an increase in agricultural grassland) should enhance the delivery of invertebrate mediated ecosystem services adjacent to arable field margins. However, high quality forb-rich field margins also supported greater numbers of canopy-active crops pests. This negative trade-off could be minimised by selecting forb species that are only attractive to beneficial invertebrate groups, but further research is required to establish the identity of such species.

## 7.3 A manual for enhancing ecosystem services within arable field margins

These guidelines are largely taken from the findings of Chapter 6 where the relative importance of a range of local and landscape factors for ecosystem service provision were considered. Flower preference data is derived from Chapter 3.

### 7.3.1 Local management to promote multiple benefits within arable field margins

#### *7.3.1.1 General guidelines*

Table 7.1 summarises the important local factors that determine ecosystem service provision and invertebrate biodiversity within arable field margins. What follows is a list of general guidelines for farmers and landowners:

- A general increase in the richness and abundance of forbs within field margin plots will enhance pollination and pest control in adjacent crop fields, and local flood alleviation capacity.

- Increasing the richness and abundance of forbs within field margin plots will also increase the abundance and richness of bumblebees, day-flying Lepidoptera and hoverflies, as well as the abundance of crop pollinators and canopy-active natural enemies of crop pests.

- Crop pests were enhanced by increasing the abundance and richness of forbs, but this problem should be ameliorated by controlling the abundance of certain flower species (see below).

- Reducing the cutting frequency to promote taller swards within field margin plots will benefit local populations of crop pollinators, bumblebees and hoverflies.

- If possible, try to avoid driving on field margin plots, especially with heavier farm machinery, as this will reduce their flood alleviation capacity by increasing soil compaction.

- If you are creating a new forb-rich field margin, the benefits to pollination of spring flowering crops will be further enhanced by situating it adjacent to a hedgerow that provides abundant floral resources earlier in the year. Hedgerows dominated by hawthorn and blackthorn would be ideal.

- Soil organic matter accumulates over time, so leaving field margins in place for as long as possible will deliver the greatest carbon storage benefits.

**Table 7.1.** Summary of the local factors influencing ecosystem service provision and invertebrate biodiversity within arable field margins ('+/-' = no effect, '+' = positive effect, blanks = factor not applicable).

| | Forb richness / abundance | Margin veg height (cm) | Reduced vehicle traffic | Hedge flower abundance | Margin age |
|---|---|---|---|---|---|
| Pest control | + | +/- | | +/- | |
| Pollination | + | +/- | | + | |
| Flood alleviation | + | | + | | |
| Soil carbon storage | +/- | | | | + |
| Crop pollinators | + | + | | +/- | |
| Canopy-active natural enemies | + | +/- | | +/- | |
| Canopy-active crop pests | + | +/- | | +/- | |
| Lepidoptera abundance | + | +/- | | +/- | |
| Lepidoptera richness | + | +/- | | +/- | |
| Bumblebee abundance | + | + | | +/- | |
| Bumblebee richness | + | + | | +/- | |
| Hoverfly abundance | + | +/- | | +/- | |
| Hoverfly richness | + | + | | +/- | |

*7.3.1.2 Beneficial forb families and species*

Table 7.2 lists the forb species that should be encouraged to promote beneficial flower-visitors such as bumblebees, solitary bees, hoverflies and parasitoid wasps. The table also lists species which are likely to benefit crop pests.

- Forb species not currently included in agri-environment seed mixes were the most attractive to bumblebees, solitary bees, hoverflies, other flies, parasitoid wasps and Lepidoptera. Attractive non-AES forb species are listed within column 'a)' in Table 7.2 below. Where possible, these species should be encouraged to promote more diverse and beneficial flower-visiting communities.

- Hogweed (*Heracleum sphondylium*) seemed to be attractive to pollen beetles and dandelion (*Taraxacum* agg.) seemed to attract wheat-stem sawflies. As such, it may not be wise to encourage these species within field margin plots, even though, when considering all flower-visitors, they were amongst the most attractive forb species overall and supported the highest number of invertebrate taxa.

- At present, field margins are floristically poor during May and early June. This could be rectified by encouraging early flowering plant species such as *Anthriscus sylvestris* and *Ranunculus repens*.

**Table 7.2.** Forb species that are (a) attractive to beneficial flower visitors and those that are (b) potentially attractive to crop pests. Species with an asterisk are those included within AES seed mixes.

| a) Attractive to beneficial flower-visitors | b) Potentially attractive to crop pests |
|---|---|
| *Anthriscus sylvestris* | *Heracleum sphondylium* |
| *Centaurea nigra** | *Taraxacum* agg. |
| *Cirsium arvense* | |
| *Cirsium vulgare* | |
| *Daucus carota** | |
| *Knautia arvensis** | |
| *Malva moschata** | |
| *Picris echioides* | |
| *Ranunculus acris** | |
| *Ranunculus repens* | |
| *Rubus fruticosus* agg. | |
| *Scorzoneroides autumnalis* | |
| *Sonchus arvensis** | |
| *Stachys sylvatica* | |
| *Tripleurospermum inodorum* | |

### 7.3.2 Landscape management to promote multiple benefits within arable field margins

- Creating smaller cropping units by planting hedgerows or creating margins across the centre of large fields will promote the dispersal of hoverflies (an important natural enemy of crop pests) across the landscape, which may have a positive effect on natural pest suppression within crop fields.

- Increasing the proportion of grassland (for livestock and/or silage) relative to the amount of arable land should increase the levels of natural pest control on your farm.

- The results of this study indicate that landscape management prescriptions to promote invertebrate mediated ecosystem services should be carried out at the farm level (*i.e.* a 1 km radius around the centre of each farm).

- However, previous studies have found that landscape management at scales larger than those used here (*e.g.* up to 3 km) are also important for farmland invertebrate populations and the ecosystem services they provide. This suggest that planning landscape management prescriptions across farms would be equally beneficial.

**7.4 Study limitations and avenues of future research**

This study used a mensurative approach, which means the results are correlative rather than causative. However, manipulative experiments corroborate that, compared to forb-poor (*i.e*. low quality) biotopes, forb-rich (*i.e.* high quality) biotopes can increase crop pollination (Blaauw and Isaacs, 2014a), natural pest control (Blaauw and Isaacs, 2015, Woodcock et al., 2016a), invertebrate biodiversity (Haaland et al., 2011), invertebrate ecosystem service providers (Carvell et al., 2007, Pywell et al., 2011) and infiltration (Fischer et al., 2015). Nonetheless, no study to date has used an experimental approach to measure whether the ecosystem service and biodiversity metrics studied here can be simultaneously enhanced by forb-rich margins. Future work should address this to provide more concrete evidence of the agronomic and ecological benefits that forb-rich field margins deliver.

A second limitation is that this study did not directly measure the contribution of high quality margins to agronomic productivity since pest control and pollination services were quantified by using proxy measurements rather than assessing these services within the standing crop. This also meant that the economic benefit of high quality margins in terms of the positive effects on yield increases (via increases in pollination and natural pest suppression) and reductions in pesticide usage (via increases in natural pest suppression) could not be calculated. Farmers would be more willing to adopt forb-rich margins if they provide a net positive economic contribution to the farm business (Bommarco et al., 2013). Therefore, studies are required that examine the full suite of economic costs and benefits of field margin creation (Whittingham, 2011).

Each of the invertebrate survey techniques used here have biases, but one consistent problem is that they measure activity rather than relative abundance (Lang, 2000, Doxon et al., 2011, Wood et al., 2015a). Consequently, the greater numbers of flower-visitors recorded within high quality margins probably reflects a redistribution of existing populations in response to more abundant floral resources (Holland et al., 2015). This tells you almost nothing about the response of flower-visitor populations (Scheper et al., 2015). However, given that most flower-visitor taxa engaged in greater levels of feeding activity within high

quality margins, forb-rich margins are likely to enhance local pollinator populations providing other resource requirements are not limiting (*e.g.* nesting habitat and larval foodplants) (Roulston and Goodell, 2011, Dennis, 2012, Carvell et al., 2015, Wood et al., 2015c). Ultimately, to establish whether the creation of forb-rich margins increase pollinator populations, studies need to adopt an experimental before-and-after control approach using molecular survey techniques (sensu Kleijn et al., 2006, Scheper et al., 2015, Wood et al., 2015c).

Finally, this study demonstrated that forb-rich field margins enhance the local abundance of agronomically damaging crop pests. Indeed, *H. sphondylium* and *Taraxacum* agg. were extremely attractive to pollen beetles and wheat-stem sawflies, respectively. At the same time, these forb species were extremely important for the wider flower-visiting community. We need to establish whether, by increasing the local activity of crop pests, forb-rich field margins elevate levels of pest damage within the adjacent crop. We also need to identify the forb species that are only attractive to beneficial invertebrates (*e.g.* crop pollinators and natural enemies). Some of this work has been done already for a handful of species (e.g. Winkler et al., 2009, Winkler et al., 2010), but it would be useful for farmers if ecologists developed a catalogue of all the plants existing within agro-ecosystems which specified the forb species to promote and the species that should be discouraged.

**7.5 Conclusion**

To meet growing food demands whilst protecting the environment, agro-ecosystems must promote ecological intensification (Bommarco et al., 2013). But this requires knowledge of the specific management prescriptions and mechanisms that enhance the biodiversity and ecological processes that mediate agricultural production (Bennett et al., 2009, Bennett et al., 2015). This study demonstrated that the creation of forb-rich field margins can enhance invertebrate biodiversity and a range of ecosystem services, including natural pest control, crop pollination and flood alleviation. Moreover, by implementing a range of additional local and landscape management prescriptions, farmers may further increase the potential of forb-rich field margins to deliver multiple ecosystem service benefits. Importantly, the present study also suggests that more consideration should be given to the forb species included within field margin seed mixes; since, certain forb species may promote crop pests, but others, which are not currently included in field margin seed mixes, are extremely attractive to several important flower-visiting taxa and/or flower during spring when field margins are floristically

poor. In order to justify removing land from cultivation at a time when food demand is increasing, ecologists need to demonstrate the multiple agronomic and environmental benefits that uncropped areas can provide (Holland et al., 2017b). Furthermore, the uptake of agri-environment schemes, such as forb-rich field margins, is likely to increase if the agronomic benefits are more consistently demonstrated (Wratten et al., 2012).

# Appendix

**Table A1.** Grid references for each of the study farms used in this project.

| Site number | Farm name | Grid reference |
|---|---|---|
| 1 | Manor Farm | SK 77213 08070 |
| 2 | Loddington | SK 79659 01312 |
| 3 | Monkton Farm | SP 88692 97003 |
| 4 | The Oaks | SP 66931 87568 |
| 5 | Lambcote Hill Farm | SP 56481 81272 |
| 6 | Stoke Plain Farm | SP 72724 50740 |
| 7 | Old Rectory Cottage | TL 02558 58951 |
| 8 | Wood End Farm | TL 10953 47024 |
| 9 | Agden Green Farm | TL 13514 66195 |
| 10 | Midloe Grange Farm | TL 16570 64725 |
| 11 | Papley Grove Farm | TL 27395 61991 |
| 12 | Hope Farm | TL 32436 62722 |
| 13 | Highfield Farm | TL 32585 41463 |
| 14 | Hay Farm | TL 34128 37203 |
| 15 | Codicote Bottom Farm | TL 20153 17787 |
| 16 | Old Park Farm | TL 44319 16007 |

**Table A2.** Margin use and cropping during the PhD study

| Study site | Margin number | Quality | Quality index score | Soil analysis 2014 | Pitfall trapping 2015 | Adjacent crop 2015 | Transects 2016 | Phytometer experiment 2016 | Egg card experiment 2016 | Sweep netting 2016 | Adjacent crop 2016 | Infiltration measure-ments 2017 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 1 | High | 44.53 | Yes | Yes | Winter Wheat | No | No | No | No | NA | Yes |
| 1 | 2 | High | 38.85 | Yes | Yes | Winter Wheat | No | No | No | No | NA | Yes |
| 1 | 3 | Low | 11.17 | Yes | Yes | Winter Wheat | No | No | No | No | NA | Yes |
| 1 | 4 | Low | 16.61 | Yes | Yes | Winter Wheat | No | No | No | No | NA | Yes |
| 1 | 5 | Low | 15.7 | Yes | Yes | Winter Wheat | No | No | No | No | NA | Yes |
| 1 | 6 | Low | 2.96 | Yes | Yes | Winter Wheat | No | No | No | No | NA | Yes |
| 2 | 7 | High | 46.15 | Yes | Yes | Winter Wheat | No | No | No | No | NA | Yes |
| 2 | 8 | High | 75.62 | Yes | Yes | Winter Wheat | No | No | No | No | NA | Yes |
| 2 | 9 | Low | 3.57 | Yes | Yes | Winter Wheat | No | No | No | No | NA | Yes |
| 2 | 10 | High | 51.56 | Yes | Yes | Winter Wheat | No | No | No | No | NA | Yes |
| 2 | 11 | Low | 20.77 | Yes | Yes | Winter Wheat | No | No | No | No | NA | Yes |
| 2 | 12 | Low | 9.57 | Yes | Yes | Winter Wheat | No | No | No | No | NA | Yes |
| 3 | 13 | High | 70.33 | Yes | Yes | Spring Oats | No | No | No | No | NA | No |
| 3 | 14 | High | 65.89 | Yes | Yes | Winter Wheat | No | No | No | No | NA | No |
| 3 | 15 | Low | 13.96 | Yes | Yes | Winter Wheat | Yes | No | No | No | Winter Wheat | Yes |
| 3 | 16 | Low | 2.93 | Yes | Yes | Spring Oats | No | No | No | No | NA | Yes |

| Study site | Margin number | Quality | Quality index score | Soil analysis 2014 | Pitfall trapping 2015 | Adjacent crop 2015 | Transects 2016 | Phytometer experiment 2016 | Egg card experiment 2016 | Sweep netting 2016 | Adjacent crop 2016 | Infiltration measure-ments 2017 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 3 | 17 | Low | 6.96 | Yes | Yes | Winter Wheat | Yes | No | No | No | Winter Wheat | Yes |
| 3 | 18 | Low | 10.45 | Yes | Yes | Winter Wheat | Yes | No | No | No | Winter Wheat | Yes |
| 4 | 19 | High | 59.41 | Yes | Yes | Winter Wheat | Yes | No | No | No | Winter Wheat | Yes |
| 4 | 20 | High | 49.38 | Yes | Yes | Winter Wheat | Yes | No | No | No | Winter Wheat | Yes |
| 4 | 21 | High | 48.78 | Yes | Yes | Winter Wheat | No | No | No | No | NA | No |
| 4 | 22 | High | 38.74 | Yes | Yes | Winter Wheat | Yes | No | No | No | Winter Wheat | Yes |
| 4 | 23 | Low | 18.4 | Yes | Yes | Winter Wheat | No | No | No | No | NA | Yes |
| 4 | 24 | Low | 13.74 | Yes | Yes | Winter Wheat | No | No | No | No | NA | Yes |
| 5 | 25 | Low | 16.2 | Yes | Yes | Winter Oats | Yes | No | No | No | Winter Wheat | Yes |
| 5 | 26 | Low | 18.13 | Yes | Yes | Winter Oats | Yes | No | No | No | Winter Wheat | Yes |
| 5 | 27 | Low | 15.75 | Yes | Yes | Winter Oats | Yes | No | No | No | Winter Wheat | Yes |
| 5 | 28 | Low | 3.28 | Yes | Yes | Winter Wheat | No | No | No | No | NA | Yes |
| 5 | 29 | Low | 15.13 | Yes | Yes | Winter Oats | No | No | No | No | NA | Yes |
| 5 | 30 | Low | 21.85 | Yes | Yes | Winter Oats | No | No | No | No | NA | Yes |
| 6 | 31 | High | 64.45 | Yes | Yes | Winter Wheat | Yes | Yes | Yes | Yes | Spring Wheat | Yes |
| 6 | 32 | High | 73.72 | Yes | Yes | Winter Wheat | Yes | No | No | No | Spring Wheat | Yes |
| 6 | 33 | High | 71.65 | Yes | Yes | Winter Wheat | No | No | No | No | NA | Yes |

| Study site | Margin number | Quality | Quality index score | Soil analysis 2014 | Pitfall trapping 2015 | Adjacent crop 2015 | Transects 2016 | Phytometer experiment 2016 | Egg card experiment 2016 | Sweep netting 2016 | Adjacent crop 2016 | Infiltration measure-ments 2017 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 6 | 34 | Low | 10.36 | Yes | Yes | Winter Wheat | Yes | No | No | No | Winter Wheat | Yes |
| 6 | 35 | Low | 20.55 | Yes | Yes | Winter Wheat | Yes | Yes | Yes | Yes | Spring Wheat | Yes |
| 6 | 36 | Low | 14.42 | Yes | Yes | Winter Wheat | Yes | No | No | No | Spring Wheat | Yes |
| 7 | 37 | High | 42.51 | Yes | Yes | Winter Wheat | Yes | No | No | No | Winter Wheat | Yes |
| 7 | 38 | High | 76.82 | Yes | Yes | Winter Wheat | No | Yes | Yes | Yes | NA | Yes |
| 7 | 39 | High | 46.74 | Yes | Yes | Spring Barley | No | No | No | No | NA | Yes |
| 7 | 40 | Low | 18.35 | Yes | Yes | Winter Wheat | Yes | No | No | No | Winter Wheat | Yes |
| 7 | 41 | Low | 7.97 | Yes | Yes | Winter Wheat | Yes | Yes | Yes | Yes | Winter Wheat | Yes |
| 7 | 42 | Low | 16.88 | Yes | Yes | Spring Barley | No | No | No | No | NA | Yes |
| 8 | 43 | Low | 11.97 | Yes | Yes | Winter Wheat | No | No | No | No | NA | Yes |
| 8 | 44 | High | 62.23 | Yes | Yes | Winter Wheat | Yes | Yes | Yes | Yes | Winter Wheat | Yes |
| 8 | 45 | High | 54.02 | Yes | Yes | Winter Wheat | Yes | No | No | No | Winter Wheat | Yes |
| 8 | 46 | Low | 14.44 | Yes | Yes | Winter Wheat | No | No | No | No | NA | Yes |
| 8 | 47 | Low | 8.69 | Yes | Yes | Winter Wheat | Yes | Yes | Yes | Yes | Winter Wheat | Yes |
| 8 | 48 | Low | 11.29 | Yes | Yes | Winter Wheat | No | No | No | No | NA | Yes |
| 9 | 49 | High | 48.39 | Yes | Yes | Winter Barley | No | No | No | No | NA | Yes |
| 9 | 50 | High | 49.01 | Yes | Yes | Winter Barley | No | No | No | No | NA | Yes |

| Study site | Margin number | Quality | Quality index score | Soil analysis 2014 | Pitfall trapping 2015 | Adjacent crop 2015 | Transects 2016 | Phytometer experiment 2016 | Egg card experiment 2016 | Sweep netting 2016 | Adjacent crop 2016 | Infiltration measure-ments 2017 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 9 | 51 | Low | 20 | Yes | Yes | Winter Wheat | Yes | No | No | No | Winter Wheat | Yes |
| 9 | 52 | Low | 13.12 | Yes | Yes | Winter Barley | No | No | No | No | NA | Yes |
| 9 | 53 | Low | 17.78 | Yes | Yes | Winter Barley | No | No | No | No | NA | Yes |
| 9 | 54 | Low | 18.66 | Yes | Yes | Winter Wheat | No | No | No | No | NA | No |
| 10 | 55 | High | 50.78 | Yes | Yes | Winter Wheat | No | No | No | No | NA | Yes |
| 10 | 56 | High | 50.78 | Yes | Yes | Winter Wheat | No | No | No | No | NA | Yes |
| 10 | 57 | High | 50.2 | Yes | Yes | Winter Wheat | No | No | No | No | NA | Yes |
| 10 | 58 | Low | 0.96 | Yes | Yes | Winter Wheat | No | No | No | No | NA | Yes |
| 10 | 59 | Low | 3.95 | Yes | Yes | Winter Wheat | No | No | No | No | NA | Yes |
| 10 | 60 | Low | 10.77 | Yes | Yes | Winter Wheat | Yes | Yes | Yes | Yes | Spring Wheat | Yes |
| 10 | 61 | High | 57.23 | No | No | NA | Yes | Yes | Yes | Yes | Spring Wheat | Yes |
| 11 | 62 | High | 63.49 | Yes | Yes | Winter Wheat | No | No | No | No | NA | Yes |
| 11 | 63 | High | 66.44 | Yes | Yes | Winter Wheat | No | No | No | No | NA | Yes |
| 11 | 64 | High | 68.6 | Yes | Yes | Winter Wheat | Yes | Yes | Yes | Yes | Winter Wheat | Yes |
| 11 | 65 | Low | 17.44 | Yes | Yes | Winter Wheat | No | No | No | No | NA | Yes |
| 11 | 66 | Low | 4.25 | Yes | Yes | Winter Wheat | No | No | No | No | NA | Yes |
| 11 | 67 | Low | 7.89 | Yes | Yes | Winter Wheat | Yes | Yes | Yes | Yes | Winter Wheat | Yes |

| Study site | Margin number | Quality | Quality index score | Soil analysis 2014 | Pitfall trapping 2015 | Adjacent crop 2015 | Transects 2016 | Phytometer experiment 2016 | Egg card experiment 2016 | Sweep netting 2016 | Adjacent crop 2016 | Infiltration measure-ments 2017 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 12 | 68 | High | 73.39 | Yes | Yes | Winter Wheat | Yes | No | No | No | Spring Barley | Yes |
| 12 | 69 | High | 64.89 | Yes | Yes | Winter Wheat | No | No | No | No | NA | Yes |
| 12 | 70 | High | 59.05 | Yes | Yes | Winter Wheat | No | No | No | No | NA | Yes |
| 12 | 71 | Low | 20.13 | Yes | Yes | Winter Wheat | Yes | No | No | No | Spring Barley | Yes |
| 12 | 72 | Low | 13.54 | Yes | Yes | Winter Wheat | No | No | No | No | NA | Yes |
| 12 | 73 | Low | 12.69 | Yes | Yes | Winter Wheat | Yes | No | No | No | Spring Barley | Yes |
| 13 | 74 | High | 39.66 | Yes | Yes | Winter Barley | No | No | No | No | NA | Yes |
| 13 | 75 | High | 36.2 | Yes | Yes | Winter Wheat | No | No | No | No | NA | Yes |
| 13 | 76 | High | 34.49 | Yes | Yes | Winter Wheat | No | No | No | No | NA | Yes |
| 13 | 77 | Low | 12.33 | Yes | Yes | Winter Barley | No | No | No | No | NA | Yes |
| 13 | 78 | Low | 16.26 | Yes | Yes | Winter Wheat | No | No | No | No | NA | Yes |
| 13 | 79 | Low | 13.26 | Yes | Yes | Winter Wheat | No | No | No | No | NA | Yes |
| 14 | 80 | High | 80.82 | Yes | Yes | Winter Wheat | Yes | Yes | Yes | Yes | Winter Barley | Yes |
| 14 | 81 | High | 76.77 | Yes | Yes | Winter Wheat | Yes | No | No | No | Winter Barley | Yes |
| 14 | 82 | High | 41.61 | Yes | Yes | Winter Wheat | No | No | No | No | NA | Yes |
| 14 | 83 | Low | 21.41 | Yes | Yes | Winter Wheat | Yes | Yes | Yes | Yes | Winter Barley | Yes |
| 14 | 84 | Low | 25.11 | Yes | Yes | Winter Beans | No | No | No | No | NA | No |

| Study site | Margin number | Quality | Quality index score | Soil analysis 2014 | Pitfall trapping 2015 | Adjacent crop 2015 | Transects 2016 | Phytometer experiment 2016 | Egg card experiment 2016 | Sweep netting 2016 | Adjacent crop 2016 | Infiltration measure-ments 2017 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 14 | 85 | Low | 22.98 | Yes | Yes | Winter Barley | Yes | No | No | No | Winter Barley | Yes |
| 15 | 86 | High | 46.36 | Yes | Yes | Winter Wheat | No | No | No | No | NA | Yes |
| 15 | 87 | High | 36.94 | Yes | Yes | Winter Wheat | No | No | No | No | NA | Yes |
| 15 | 88 | High | 64.52 | Yes | Yes | Winter Wheat | No | No | No | No | NA | Yes |
| 15 | 89 | Low | 8.17 | Yes | Yes | Winter Wheat | Yes | Yes | Yes | Yes | Winter Barley | Yes |
| 15 | 90 | Low | 7.19 | Yes | Yes | Winter Wheat | Yes | No | No | No | Spring Barley | Yes |
| 15 | 91 | Low | 7.57 | Yes | Yes | Winter Wheat | Yes | No | No | No | Spring Barley | Yes |
| 15 | 92 | High | 34.92 | No | No | NA | Yes | Yes | Yes | Yes | Winter Barley | Yes |
| 16 | 93 | High | 45.55 | Yes | Yes | Winter Wheat | No | No | No | No | NA | Yes |
| 16 | 94 | High | 51.65 | Yes | Yes | Winter Wheat | Yes | No | No | No | Winter Wheat | Yes |
| 16 | 95 | High | 81.01 | Yes | Yes | Winter Wheat | Yes | Yes | Yes | Yes | Winter Wheat | Yes |
| 16 | 96 | Low | 7.33 | Yes | Yes | Winter Wheat | Yes | No | No | No | Winter Wheat | Yes |
| 16 | 97 | Low | 18.32 | Yes | Yes | Winter Wheat | Yes | Yes | Yes | Yes | Winter Wheat | Yes |
| 16 | 98 | High | 39.79 | Yes | Yes | Winter Wheat | No | No | No | No | NA | Yes |

**Table A3.** Linear and general linear mixed-effect models (LMMs and GLMMs, respectively) used during Chapter 3 data analysis.

**a) Objective 1: Is the quality index a valid and reliable measure of flower-visitor foraging habitat?**

*i) Differences in floral resources recorded within high and low quality margin plots during transect surveys in 2016*

| Location of variable measurement | Response variable | Model[1] | Error structure | Transformation | Fixed effects[2] | Random effect |
|---|---|---|---|---|---|---|
| Margin | Floral richness | GLMMs | Poisson (log-link) | _ | Q | 1\| Site |
| Margin | Number of floral units | GLMMs | Negative binomial (log-link) | _ | Q | 1\| Site |

*ii) Differences in the proportion of feeding observations recorded within high and low quality margin plots during transect surveys in 2016*

| Location of variable measurement | Response variable | Model[1] | Error structure | Transformation | Fixed effects[2] | Random effect |
|---|---|---|---|---|---|---|
| Margin | Proportion of honeybees feeding | GLMMs | Negative binomial (log-link) | _ | Q | 1\| Site |
| Margin | Proportion of bumblebees feeding | LMMs | Gaussian | Arcsine | Q | 1\| Site |
| Margin | Proportion of solitary bees feeding | LMMs | Gaussian | Arcsine | Q | 1\| Site |
| Margin | Proportion of parasitoid wasps feeding | LMMs | Gaussian | _ | Q | 1\| Site |
| Margin | Proportion of sawflies feeding | LMMs | Gaussian | Arcsine | Q | 1\| Site |
| Margin | Proportion of Lepidoptera feeding | GLMMs | Negative binomial (log-link) | _ | Q | 1\| Site |
| Margin | Proportion of hoverflies feeding | LMMs | Gaussian | _ | Q | 1\| Site |
| Margin | Proportion of non-Syrphid Diptera feeding | LMMs | Gaussian | _ | Q | 1\| Site |
| Margin | Proportion of beetles feeding | LMMs | Gaussian | Arcsine | Q | 1\| Site |

*iii) Differences in the abundance of specific flower-visitor taxa between high and low quality margin plots during transect surveys in 2016*

| Location of variable measurement | Response variable | Model[1] | Error structure | Transformation | Fixed effects[2] | Random effect |
|---|---|---|---|---|---|---|
| Margin | Honeybee abundance | LMMs | Gaussian | ln(x+1) | Q | 1\| Site |
| Margin | Bumblebee abundance | GLMMs | Negative binomial (log-link) | _ | Q | 1\| Site |
| Margin | Solitary bee abundance | LMMs | Gaussian | _ | Q | 1\| Site |
| Margin | Parasitoid wasp abundance | LMMs | Gaussian | sqrt | Q | 1\| Site |
| Margin | Sawfly abundance | LMMs | Gaussian | ln(x+1) | Q | 1\| Site |
| Margin | Lepidoptera abundance | GLMMs | Negative binomial (log-link) | _ | Q | 1\| Site |
| Margin | Hoverfly abundance | LMMs | Gaussian | ln(x) | Q | 1\| Site |
| Margin | Non-Syrphid Diptera abundance | GLMMs | Negative binomial (log-link) | _ | Q | 1\| Site |
| Margin | Beetle abundance | LMMs | Gaussian | ln(x) | Q | 1\| Site |

[1] Model abbreviations: GLMMs, generalised linear mixed-effect models; LMMs, linear mixed-effect models.

[2] Fixed effect abbreviations: Q, field margin quality (low/high).

**b) Objective 2: Do AES arable field margins currently provide sufficient foraging resources for flower-visiting insects?**

*i) Effect of season on floral resources*

| Location of variable measurement | Response variable | Model[1] | Error structure | Transformation | Fixed effects[2] | Random effect |
|---|---|---|---|---|---|---|
| Margin | Floral richness | GLMMs | Negative binomial (log-link) | _ | S | 1\| Site |
| Margin | Number of floral units | LMMs | Gaussian | ln(x) | S | 1\| Site |

**c) Objective 3: Do high quality field margins promote ecosystem services and biodiversity more effectively than low quality field margins?**

*i) Ecosystem services*

| Location of variable measurement | Response variable | Model[1] | Error structure | Transformation | Fixed effects[2] | Random effect |
|---|---|---|---|---|---|---|
| Crop edge and interior | Calliphora canopy predation index (0-1) | LMMs | Gaussian | sqrt | Q + CP + Q x CP | 1\| Site |
| Crop edge and interior | Ephestia canopy predation index (0-1) | LMMs | Gaussian | arcsine | Q + CP + Q x CP | 1\| Site |
| Crop edge and interior | Mean number of fertilised achenes produced | LMMs | Gaussian | sqrt | Q + CP + Q x CP | 1\| Site |
| Crop edge and interior | Mean number of fruits produced | GLMMs | Negative binomial (log-link) | _ | Q + CP + Q x CP | 1\| Site |
| Margin | $K_{fs}$ (mm $h^{-1}$) | GLMMs | Negative binomial (log-link) | _ | Q | 1\| Site |
| Margin | Soil organic matter (%) | LMMs | Gaussian | sqrt | Q | 1\| Site |
| Margin | Soil nitrogen (0-6 cm) (kg N $m^{-2}$ soil) | GLMMs | Poisson (log-link) | _ | Q | 1\| Site |
| Margin | Soil carbon (0-6 cm) (kg C $m^{-2}$ soil) | GLMMs | Negative binomial (log-link) | _ | Q | 1\| Site |

*ii) Invertebrate ecosystem service providers*

| Location of variable measurement | Response variable | Model[1] | Error structure | Transformation | Fixed effects[2] | Random effect |
|---|---|---|---|---|---|---|
| Margin | Crop pollinators | LMMs | Gaussian | ln(x) | Q + S + Q x S | 1\| Site |
| Margin | Aerial natural enemies | LMMs | Gaussian | sqrt | Q + S + Q x S | 1\| Site |
| Margin | Aerial crop pests | LMMs | Gaussian | ln(x) | Q + S + Q x S | 1\| Site |
| Margin | Epigeal natural enemies | GLMMs | Negative binomial (log-link) | _ | Q | 1\| Site |
| Margin | Epigeal crop pests | LMMs | Gaussian | ln(x) | Q | 1\| Site |
| Margin, crop edge and crop interior | Canopy-active natural enemies | GLMMs | Negative binomial (log-link) | _ | Q + SP + Q x SP | 1\| Site |
| Margin, crop edge and crop interior | Canopy-active crop pests | GLMMs | Negative binomial (log-link) | _ | Q + SP + Q x SP | 1\| Site |

*iii) Invertebrate biodiversity*

| Location of variable measurement | Response variable | Model[1] | Error structure | Transformation | Fixed effects[2] | Random effect |
|---|---|---|---|---|---|---|
| Margin | Number of forb species in flower (along transects) | LMMs | Gaussian | sqrt | Q + S + Q x S | 1\| Site |
| Margin | Number of floral units (along transects) | LMMs | Gaussian | ln(x) | Q + S + Q x S | 1\| Site |
| Margin | Lepidoptera abundance | LMMs | Gaussian | ln(x+1) | Q + S + Q x S | 1\| Site |
| Margin | Lepidoptera richness | LMMs | Gaussian | sqrt | Q + S + Q x S | 1\| Site |
| Margin | Bumblebee abundance | LMMs | Gaussian | ln(x+1) | Q + S + Q x S | 1\| Site |
| Margin | Bumblebee richness | LMMs | Gaussian | _ | Q + S + Q x S | 1\| Site |
| Margin | Hoverfly abundance | LMMs | Gaussian | sqrt | Q + S + Q x S | 1\| Site |
| Margin | Hoverfly richness | LMMs | Gaussian | _ | Q + S + Q x S | 1\| Site |
| Margin | Transect taxonomic richness | LMMs | Gaussian | _ | Q + S + Q x S | 1\| Site |
| Margin | Pitfall trap taxonomic richness | LMMs | Gaussian | _ | Q | 1\| Site |
| Margin, crop edge and crop interior | Sweep net taxonomic richness | LMMs | Gaussian | _ | Q + SP + Q x SP | 1\| Site |

[1] Model abbreviations: GLMMs, generalized linear mixed models; LMMs, linear mixed models.

[2] Fixed effect abbreviations: Q, field margin quality (low/high); CP, crop position (edge/interior); S, transect survey season (early/late); SP, sweep net position (margin/edge/interior)

**d) Objective 4: Does increasing field margin quality promote ecological multifunctionality?**

| Location of variable measurement | Response variable | Model[1] | Error structure | Transformation | Fixed effects[2] | Random effect |
|---|---|---|---|---|---|---|
| Crop edge and crop interior | Calliphora larvae predation index (0-1) | LMMs | Gaussian | sqrt | Q | 1\| Site |
| Crop edge and crop interior | Ephestia egg predation index (0-1) | LMMs | Gaussian | _ | Q | 1\| Site |
| Crop edge and crop interior | Mean number of fertilised achenes produced | LMMs | Gaussian | ln(x) | Q | 1\| Site |
| Crop edge and crop interior | Mean number of strawberry fruits produced | LMMs | Gaussian | ln(x) | Q | 1\| Site |
| Margin | $K_{fs}$ (mm $h^{-1}$) | LMMs | Gaussian | ln(x) | Q | 1\| Site |
| Margin | Soil organic matter (%) | LMMs | Gaussian | ln(x) | Q | 1\| Site |
| Margin | Soil nitrogen (0-6 cm) (kg N m−2 soil) | LMMs | Gaussian | ln(x) | Q | 1\| Site |
| Margin | Soil carbon (0-6 cm) (kg C $m^{-2}$ soil) | LMMs | Gaussian | sqrt | Q | 1\| Site |
| Margin | Crop pollinators | LMMs | Gaussian | ln(x) | Q | 1\| Site |
| Margin | Aerial natural enemies | LMMs | Gaussian | ln(x) | Q | 1\| Site |
| Margin | Aerial crop pests | LMMs | Gaussian | ln(x) | Q | 1\| Site |
| Margin | Epigeal natural enemies | LMMs | Gaussian | ln(x) | Q | 1\| Site |
| Margin | Epigeal crop pests | LMMs | Gaussian | ln(x) | Q | 1\| Site |
| Margin, crop edge and crop interior | Canopy-active natural enemies | LMMs | Gaussian | sqrt | Q | 1\| Site |
| Margin, crop edge and crop interior | Canopy-active crop pests | LMMs | Gaussian | _ | Q | 1\| Site |
| Margin | Lepidoptera abundance | LMMs | Gaussian | sqrt | Q | 1\| Site |
| Margin | Lepidoptera richness | LMMs | Gaussian | _ | Q | 1\| Site |
| Margin | Bumblebee abundance | LMMs | Gaussian | sqrt | Q | 1\| Site |
| Margin | Bumblebee richness | LMMs | Gaussian | _ | Q | 1\| Site |
| Margin | Hoverfly abundance | LMMs | Gaussian | ln(x) | Q | 1\| Site |
| Margin | Hoverfly richness | LMMs | Gaussian | _ | Q | 1\| Site |
| Margin | Transect taxonomic richness | LMMs | Gaussian | _ | Q | 1\| Site |
| Margin | Pitfall trap taxonomic richness | LMMs | Gaussian | _ | Q | 1\| Site |
| Margin, crop edge and crop interior | Sweep net taxonomic richness | LMMs | Gaussian | _ | Q | 1\| Site |

[1]Model abbreviations: GLMMs, generalized linear mixed models; LMMs, linear mixed models.

[2]Fixed effect abbreviations: Q, field margin quality (low/high).

**Table A4.** Linear and General linear models (LMs and GLMs, respectively) used during Chapter 4 data analysis

*i) The effect of landscape composition on insect mediated ecosystem services*

| Location of variable measurement | Response variable | Model[1] | Error structure | Transformation | Fixed effects |
|---|---|---|---|---|---|
| Crop edge and interior | *Calliphora* larvae predation index (0-1) | LMs | Guassian | sqrt | Agricultural grassland % 1 km |
| Crop edge and interior | *Ephestia* egg predation index (0-1) | LMs | Guassian | _ | Arable % 1 km |
| Crop edge and interior | Mean number of fertilised achenes produced | LMs | Guassian | _ | Agricultural grassland % 250 m |
| | | | | | Uncropped % 250 m |
| Crop edge and interior | Mean number of fruits produced | LMs | Guassian | ln(x) | Uncropped % 1 km |

*ii) The effect of landscape composition on invertebrate ecosystem service providers*

| Location of variable measurement | Response variable | Model[1] | Error structure | Transformation | Fixed effects |
|---|---|---|---|---|---|
| Margin | Crop pollinators | GLMs | Negative binomial (log-link) | _ | Season x Arable % 250 m |
| Margin | Aerial natural enemies | LMs | Guassian | ln(x) | Season |
| | | | | | Arable % 1 km |
| Margin | Aerial crop pests | GLMs | Negative binomial (log-link) | _ | Season |
| Margin | Epigeal natural enemies | GLMs | Negative binomial (log-link) | _ | Uncropped % 250 m |
| Margin | Epigeal crop pests | LMs | Guassian | _ | No significant factor |
| Margin, crop edge and crop interior | Canopy-active natural enemies | GLMs | Negative binomial (log-link) | _ | Sweep net position |
| | | | | | Agricultural grassland % 1 km |
| Margin, crop edge and crop interior | Canopy-active crop pests | GLMs | Negative binomial (log-link) | _ | Sweep net position |

*iii) The effect of landscape composition on biodiversity*

| Location of variable measurement | Response variable | Model[1] | Error structure | Transformation | Fixed effects |
|---|---|---|---|---|---|
| Margin | Lepidoptera abundance | GLMs | Negative binomial (log-link) | _ | Season |
| Margin | Lepidoptera richness | GLMs | Negative binomial (log-link) | _ | Season |
| Margin | Bumblebee abundance | GLMs | Negative binomial (log-link) | _ | Season |
| | | | | | Season x Agricultural grassland % 1 km |
| Margin | Bumblebee richness | GLMs | Poisson (log-link) | _ | Survey season |
| Margin | Hoverfly abundance | GLMs | Negative binomial (log-link) | _ | Season |
| Margin | Hoverfly richness | GLMs | Negative binomial (log-link) | _ | Season |
| Margin | Transect taxonomic richness | LMs | Guassian | _ | Season |
| | | | | | Urban % 1 km |
| | | | | | Agricultural grassland % 1 km |
| Margin | Pitfall trap taxonomic richness | LMs | Guassian | _ | Uncropped % 1 km |
| Margin, crop edge and crop interior | Sweep net taxonomic richness | GLMs | Negative binomial (log-link) | _ | Sweep net position |

[1] Model abbreviations: GLMs, general linear models; LMs, linear models.

**Table A5.** Pearson correlations between landscape composition metrics surrounding margins used during (a) pest control and pollination assays, (b) transect surveys, (c) pitfall trapping and (d) sweep netting. Yellow cells indicate collinear relationships above the 0.65 threshold.

*a) Pest control and pollination assays*

| | Arable 1k | Agricultural grassland 1k | Urban 1k | Uncropped 1k | Arable 500m | Agricultural grassland 500m | Urban 500m | Uncropped 500m | Arable 250m | Agricultural grassland 250m | Urban 250m |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Agricultural grassland 1k | -.949** | | | | | | | | | | |
| Urban 1k | -.645** | .531** | | | | | | | | | |
| Uncropped 1k | -.448* | 0.248 | -0.068 | | | | | | | | |
| Arable 500m | .719** | -.681** | -.489** | -0.299 | | | | | | | |
| Agricultural grassland 500m | -.808** | .838** | 0.309 | .384* | -.847** | | | | | | |
| Urban 500m | -.404* | 0.331 | .544** | 0.040 | -.816** | .411* | | | | | |
| Uncropped 500m | -0.044 | -0.065 | -0.011 | 0.330 | -0.245 | 0.109 | 0.073 | | | | |
| Arable 250m | .516** | -.505** | -0.112 | -.406* | .881** | -.835** | -.585** | -.372* | | | |
| Agricultural grassland 250m | -0.260 | 0.257 | -0.138 | .384* | -.610** | .678** | 0.261 | .407* | -.859** | | |
| Urban 250m | -.416* | .413* | .448* | -0.035 | -.763** | .475** | .877** | -0.095 | -.595** | 0.252 | |
| Uncropped 250m | -.563** | .538** | 0.184 | .414* | -.563** | .565** | 0.317 | 0.327 | -.552** | 0.178 | 0.248 |

**. Correlation is significant at the 0.01 level (2-tailed); *. Correlation is significant at the 0.05 level (2-tailed).

*b) Transect surveys*

| | Arable 1k | Agricultural grassland 1k | Urban 1k | Uncropped 1k | Arable 500m | Agricultural grassland 500m | Urban 500m | Uncropped 500m | Arable 250m | Agricultural grassland 250m | Urban 250m |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Agricultural grassland 1k | -.942** | | | | | | | | | | |
| Urban 1k | 0.085 | -.250* | | | | | | | | | |
| Uncropped 1k | -.284* | 0.016 | -0.154 | | | | | | | | |
| Arable 500m | .804** | -.789** | 0.081 | -0.130 | | | | | | | |
| Agricultural grassland 500m | -.800** | .886** | -0.197 | -0.120 | -.890** | | | | | | |
| Urban 500m | -0.124 | 0.021 | .472** | 0.010 | -.400** | 0.095 | | | | | |
| Uncropped 500m | -0.119 | -0.069 | -0.137 | .714** | -0.206 | -0.145 | 0.027 | | | | |
| Arable 250m | .555** | -.557** | 0.178 | -0.135 | .822** | -.699** | -.375** | -0.218 | | | |
| Agricultural grassland 250m | -.505** | .595** | -0.205 | -0.138 | -.752** | .815** | 0.151 | -0.104 | -.869** | | |
| Urban 250m | -0.172 | 0.086 | .285* | 0.084 | -.366** | 0.109 | .857** | 0.018 | -.399** | 0.146 | |
| Uncropped 250m | -0.158 | 0.015 | -0.138 | .573** | -0.164 | -0.128 | 0.124 | .734** | -.323** | -0.136 | 0.118 |

**. Correlation is significant at the 0.01 level (2-tailed); *. Correlation is significant at the 0.05 level (2-tailed).

*c) Pitfall trapping*

| | Arable 1k | Agricultural grassland 1k | Urban 1k | Uncropped 1k | Arable 500m | Agricultural grassland 500m | Urban 500m | Uncropped 500m | Arable 250m | Agricultural grassland 250m | Urban 250m |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Agricultural grassland 1k | -.908** | | | | | | | | | | |
| Urban 1k | -0.059 | -0.185 | | | | | | | | | |
| Uncropped 1k | -.213* | -0.143 | 0.013 | | | | | | | | |
| Arable 500m | .763** | -.686** | -0.119 | -0.129 | | | | | | | |
| Agricultural grassland 500m | -.705** | .816** | -0.100 | -.252* | -.824** | | | | | | |
| Urban 500m | -0.151 | 0.020 | .607** | -0.044 | -.451** | .206* | | | | | |
| Uncropped 500m | -0.148 | -0.138 | 0.041 | .783** | -.272** | -.209* | 0.003 | | | | |
| Arable 250m | .519** | -.470** | -0.089 | -0.072 | .818** | -.621** | -.405** | -.290** | | | |
| Agricultural grassland 250m | -.510** | .597** | -0.010 | -.246* | -.737** | .823** | .273** | -0.181 | -.794** | | |
| Urban 250m | -0.104 | -0.051 | .559** | 0.058 | -.303** | 0.036 | .807** | 0.079 | -.326** | 0.101 | |
| Uncropped 250m | -0.115 | -0.045 | -0.038 | .478** | -.229* | -0.149 | 0.004 | .760** | -.459** | -0.133 | 0.051 |

**. Correlation is significant at the 0.01 level (2-tailed); *. Correlation is significant at the 0.05 level (2-tailed).

*d) Sweep netting*

| | Arable 1k | Agricultural grassland 1k | Urban 1k | Uncropped 1k | Arable 500m | Agricultural grassland 500m | Urban 500m | Uncropped 500m | Arable 250m | Agricultural grassland 250m | Urban 250m |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Agricultural grassland 1k | -.949** | | | | | | | | | | |
| Urban 1k | -.645** | .531** | | | | | | | | | |
| Uncropped 1k | -.448** | 0.248 | -0.068 | | | | | | | | |
| Arable 500m | .719** | -.681** | -.489** | -.299* | | | | | | | |
| Agricultural grassland 500m | -.808** | .838** | .309* | .384** | -.847** | | | | | | |
| Urban 500m | -.404** | .331* | .544** | 0.040 | -.816** | .411** | | | | | |
| Uncropped 500m | -0.044 | -0.065 | -0.011 | .330* | -0.245 | 0.109 | 0.073 | | | | |
| Arable 250m | .516** | -.505** | -0.112 | -.406** | .881** | -.835** | -.585** | -.372** | | | |
| Agricultural grassland 250m | -0.260 | 0.257 | -0.138 | .384** | -.610** | .678** | 0.261 | .407** | -.859** | | |
| Urban 250m | -.416** | .413** | .448** | -0.035 | -.763** | .475** | .877** | -0.095 | -.595** | 0.252 | |
| Uncropped 250m | -.563** | .538** | 0.184 | .414** | -.563** | .565** | .317* | .327* | -.552** | 0.178 | 0.248 |

**. Correlation is significant at the 0.01 level (2-tailed); *. Correlation is significant at the 0.05 level (2-tailed).

**Table A6.** Linear and General linear models (LMs and GLMs, respectively) used during Chapter 5 data analysis.

| *i) The effect of landscape configuration on insect mediated ecosystem services* | | | | | |
|---|---|---|---|---|---|
| **Location of variable measurement** | **Response variable** | **Model[1]** | **Error structure** | **Transformation** | **Fixed effects** |
| Crop edge and interior | *Calliphora* larvae predation index (0-1) | LMs | Guassian | sqrt | Shannon landscape diversity 1 km |
| Crop edge and interior | *Ephestia* egg predation index (0-1) | LMs | Guassian | _ | Shannon landscape diversity 1 km |
| Crop edge and interior | Mean number of fertilised achenes per strawberry | GLMs | Negative binomial (log-link) | _ | Uncropped patch density 250 m |
| Crop edge and interior | Mean number of strawberry fruits produced | GLMs | Negative binomial (log-link) | _ | No significant factor |
| *ii) The effect of landscape configuration on invertebrate ecosystem service providers* | | | | | |
| **Location of variable measurement** | **Response variable** | **Model[1]** | **Error structure** | **Transformation** | **Fixed effects** |
| Margin | Crop pollinators | GLMs | Negative binomial (log-link) | _ | Survey season |
| Margin | Aerial natural enemies | GLMs | Negative binomial (log-link) | _ | Survey season |
| | | | | | Shape index 1 km |
| Margin | Aerial crop pests | GLMs | Negative binomial (log-link) | _ | Survey season |
| Margin | Epigeal natural enemies | GLMs | Negative binomial (log-link) | _ | No significant factor |
| Margin | Epigeal crop pests | GLMs | Negative binomial (log-link) | _ | No significant factor |
| Margin, crop edge and crop interior | Canopy-active natural enemies | GLMs | Negative binomial (log-link) | _ | Sweep net position |
| | | | | | Shape index 500 m |
| Margin, crop edge and crop interior | Canopy-active crop pests | GLMs | Negative binomial (log-link) | _ | Sweep net position |
| *iii) The effect of landscape configuration on biodiversity* | | | | | |
| **Location of variable measurement** | **Response variable** | **Model[1]** | **Error structure** | **Transformation** | **Fixed effects** |
| Margin | Lepidoptera abundance | GLMs | Negative binomial (log-link) | _ | Survey season |
| Margin | Lepidoptera richness | GLMs | Negative binomial (log-link) | _ | Survey season |
| Margin | Bumblebee abundance | GLMs | Negative binomial (log-link) | _ | Survey season |
| Margin | Bumblebee richness | GLMs | Poisson (log-link) | _ | Survey season |
| Margin | hoverfly abundance | GLMs | Negative binomial (log-link) | _ | Survey season |
| | | | | | Shape index 1 km |
| Margin | hoverfly richness | GLMs | Negative binomial (log-link) | _ | Survey season |
| Margin | Transect taxonomic richness | LMs | Guassian | _ | Survey season |
| | | | | | Shape index 500 m |
| Margin | Pitfall trap taxonomic richness | GLMs | Negative binomial (log-link) | _ | No significant factor |
| Margin, crop edge and crop interior | Sweep net taxonomic richness | GLMs | Negative binomial (log-link) | _ | Sweep net position |

[1] Model abbreviations: GLMs, general linear models; LMs, linear models.

**Table A7.** Pearson correlations between landscape complexity and connectivity metrics surrounding margins used during (a) pest control and pollination assays, (b) transect surveys, (c) pitfall trapping and (d) sweep netting. Yellow cells indicate collinear relationships above the 0.65 threshold.

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*a) Pest control and pollination assays*

| | Shannon diversity 1 km | Shape Index 1 km | Uncropped connectance index 1 km | Shannon diversity 500 m | Shape Index 500 m | Uncropped connectance index 500 m | Shannon diversity 250 m | Shape Index 250 m |
|---|---|---|---|---|---|---|---|---|
| Shape Index 1 km | -.569** | | | | | | | |
| Uncropped connectance index 1 km | -.703** | .416* | | | | | | |
| Shannon diversity 500 m | .648** | -0.135 | -.430* | | | | | |
| Shape Index 500 m | -.448* | .849** | 0.305 | -0.251 | | | | |
| Uncropped connectance index 500 m | -0.210 | -0.054 | 0.117 | -.620** | 0.083 | | | |
| Shannon diversity 250 m | .405* | 0.082 | -.412* | .896** | -0.013 | -.605** | | |
| Shape Index 250 m | -0.267 | -0.078 | -0.024 | -.403* | 0.222 | 0.208 | -0.224 | |
| Uncropped connectance index 250 m | -0.173 | 0.181 | 0.187 | -0.330 | 0.346 | 0.152 | -0.184 | -0.020 |

**. Correlation is significant at the 0.01 level (2-tailed); *. Correlation is significant at the 0.05 level (2-tailed).

*b) Transect surveys*

| | Shannon diversity 1 km | Shape Index 1 km | Uncropped connectance index 1 km | Shannon diversity 500 m | Shape Index 500 m | Uncropped connectance index 500 m | Shannon diversity 250 m | Shape Index 250 m |
|---|---|---|---|---|---|---|---|---|
| Shape Index 1 km | -.288** | | | | | | | |
| Uncropped connectance index 1 km | -.678** | .207* | | | | | | |
| Shannon diversity 500 m | .641** | -0.056 | -.453** | | | | | |
| Shape Index 500 m | -.431** | .451** | .264** | -.354** | | | | |
| Uncropped connectance index 500 m | -.206* | -0.014 | 0.150 | -.475** | 0.140 | | | |
| Shannon diversity 250 m | .461** | 0.090 | -.326** | .811** | -.207* | -.384** | | |
| Shape Index 250 m | -.386** | 0.115 | .362** | -.513** | .336** | 0.170 | -.373** | |
| Uncropped connectance index 250 m | 0.083 | 0.104 | -0.031 | 0.093 | 0.105 | -0.082 | 0.167 | -0.079 |

**. Correlation is significant at the 0.01 level (2-tailed); *. Correlation is significant at the 0.05 level (2-tailed).

*c) Pitfall trapping*

| | Shannon diversity 1 km | Shape Index 1 km | Uncropped connectance index 1 km | Shannon diversity 500 m | Shape Index 500 m | Uncropped connectance index 500 m | Shannon diversity 250 m | Shape Index 250 m |
|---|---|---|---|---|---|---|---|---|
| Shape Index 1 km | -.472** | | | | | | | |
| Uncropped connectance index 1 km | -.725** | .445** | | | | | | |
| Shannon diversity 500 m | .648** | -0.029 | -.474** | | | | | |
| Shape Index 500 m | -.468** | .605** | .342** | -.318** | | | | |
| Uncropped connectance index 500 m | -0.200 | -0.219 | 0.093 | -.602** | 0.173 | | | |
| Shannon diversity 250 m | .361** | 0.171 | -.306** | .838** | -0.027 | -.566** | | |
| Shape Index 250 m | -.273* | -0.034 | 0.187 | -.456** | .255* | .234* | -.311** | |
| Uncropped connectance index 250 m | 0.019 | 0.071 | -0.064 | -0.010 | .289** | 0.011 | 0.125 | -0.066 |

**. Correlation is significant at the 0.01 level (2-tailed); *. Correlation is significant at the 0.05 level (2-tailed).

*d) Sweep netting*

| | Shannon diversity 1 km | Shape Index 1 km | Uncropped connectance index 1 km | Shannon diversity 500 m | Shape Index 500 m | Uncropped connectance index 500 m | Shannon diversity 250 m | Shape Index 250 m |
|---|---|---|---|---|---|---|---|---|
| Shape Index 1 km | -.569** | | | | | | | |
| Uncropped connectance index 1 km | -.703** | .416* | | | | | | |
| Shannon diversity 500 m | .648** | -0.135 | -.430* | | | | | |
| Shape Index 500 m | -.448* | .849** | 0.305 | -0.251 | | | | |
| Uncropped connectance index 500 m | -0.210 | -0.054 | 0.117 | -.620** | 0.083 | | | |
| Shannon diversity 250 m | .405* | 0.082 | -.412* | .896** | -0.013 | -.605** | | |
| Shape Index 250 m | -0.267 | -0.078 | -0.024 | -.403* | 0.222 | 0.208 | -0.224 | |
| Uncropped connectance index 250 m | -0.173 | 0.181 | 0.187 | -0.330 | 0.346 | 0.152 | -0.184 | -0.020 |

**. Correlation is significant at the 0.01 level (2-tailed); *. Correlation is significant at the 0.05 level (2-tailed).

**Table A8.** Linear and general linear mixed-effect models (LMMs and GLMMs, respectively) used during Chapter 6 data analysis.

**a) Objective 1: To determine the principle factors regulating ecosystem service provision, the abundance of invertebrate ecosystem service providers and the amount of invertebrate biodiversity supported by arable field margins**

*i) Ecosystem services*

| Location of variable measurement | Response variable | Model[1] | Error structure | Transformation | Fixed effects[2] | Random effect |
|---|---|---|---|---|---|---|
| Crop edge and interior | Calliphora canopy predation index (0-1) | LMMs | Gaussian | sqrt | Q + AG1 | 1\| Site |
| Crop edge and interior | Ephestia canopy predation index (0-1) | LMMs | Gaussian | ln(x) | Q + AR1 | 1\| Site |
| Crop edge and interior | Mean number of fertilised achenes produced | LMMs | Gaussian | sqrt | Q + BF | 1\| Site |
| Crop edge and interior | Mean number of fruits produced | LMMs | Gaussian | _ | Q + UC1 | 1\| Site |
| Margin | $K_{fs}$ (mm $h^{-1}$) | LMMs | Gaussian | ln(x) | Q + VT | 1\| Site |
| Margin | Soil organic matter (%) | LMMs | Gaussian | ln(x) | MW | 1\| Site |

*ii) Ecosystem service providers*

| Location of variable measurement | Response variable | Model[1] | Error structure | Transformation | Fixed effects[2] | Random effect |
|---|---|---|---|---|---|---|
| Margin | Crop pollinators | LMMs | Gaussian | ln(x) | Q + S + Q x S + VH | 1\| Site |
| Margin, crop edge and crop interior | Canopy-active natural enemies | GLMMs | Negative binomial (log-link) | _ | Q + SP + AG1 | 1\| Site |
| Margin, crop edge and crop interior | Canopy-active crop pests | GLMMs | Negative binomial (log-link) | _ | Q + SP + Q x SP | 1\| Site |

*iii) Biodiversity*

| Location of variable measurement | Response variable | Model[1] | Error structure | Transformation | Fixed effects[2] | Random effect |
|---|---|---|---|---|---|---|
| Margin | Lepidoptera abundance | LMMs | Gaussian | ln(x) | Q + S + Q x S | 1\| Site |
| Margin | Lepidoptera richness | LMMs | Gaussian | sqrt | Q + S + Q x S | 1\| Site |
| Margin | Bumblebee abundance | LMMs | Gaussian | sqrt | Q + S + Q x S + VH | 1\| Site |
| Margin | Bumblebee richness | LMMs | Gaussian | _ | Q + S + VH | 1\| Site |
| Margin | Hoverfly abundance | LMMs | Gaussian | sqrt | Q + S + Q x S + SI1 | 1\| Site |
| Margin | Hoverfly richness | LMMs | Gaussian | _ | Q + S + Q x S + VH | 1\| Site |

[1] Model abbreviations: GLMMs, generalised linear mixed-effect models; LMMs, linear mixed-effect models.

[2] Fixed effect abbreviations: Q, field margin quality (low/high); S, transect survey season (early/late); SP, sweep net position (margin/edge/interior);VH, margin vegetation height (cm); SI1, shape index at 1 km; AG1, % agricultural grassland at 1 km; MW, margin width (m); VT, level of farm vehicle traffic (none/light/intermediate/heavy); UC1, % uncropped land at 1 km; BF, length of adjacent hedgerow in flower (m); AR1, % arable land at 1 km.

**Objective 2: To establish the most important vegetative components of margin quality for promoting ecosystem multifunctionality within arable field margins**

*i) Ecosystem services*

| Location of variable measurement | Response variable | Model[1] | Error structure | Transformation | Fixed effects | Random effect |
|---|---|---|---|---|---|---|
| Crop edge and interior | Calliphora canopy predation index (0-1) | LMMs | Gaussian | _ | % cover of other forbs | 1\| Site |
| Crop edge and interior | Ephestia canopy predation index (0-1) | LMMs | Gaussian | sqrt | % cover of other forbs | 1\| Site |
| Crop edge and interior | Mean number of fertilised achenes produced | LMMs | Gaussian | ln(x) | Total forb richness | 1\| Site |
| | | | | | % cover of Asteraceae | |
| Crop edge and interior | Mean number of fruits produced | GLMMs | Negative binomial (log-link) | _ | % cover of Asteraceae | 1\| Site |
| | | | | | Total forb richness | |
| Margin | $K_{fs}$ (mm $h^{-1}$) | GLMMs | Negative binomial (log-link) | _ | Total forb cover (%) | 1\| Site |

*ii) Ecosystem service providers*

| Location of variable measurement | Response variable | Model[1] | Error structure | Transformation | Fixed effects | Random effect |
|---|---|---|---|---|---|---|
| Margin | Crop pollinators | GLMMs | Negative binomial (log-link) | _ | Total forb cover (%) | 1\| Site |
| | | | | | % cover of Asteraceae | |
| Margin, crop edge and crop interior | Canopy-active natural enemies | GLMMs | Negative binomial (log-link) | _ | % cover of Fabaceae | 1\| Site |
| Margin, crop edge and crop interior | Canopy-active crop pests | LMMs | Gaussian | _ | % cover of Asteraceae | 1\| Site |
| | | | | | Forb richness | |

*iii) Biodiversity*

| Location of variable measurement | Response variable | Model[1] | Error structure | Transformation | Fixed effects | Random effect |
|---|---|---|---|---|---|---|
| Margin | Lepidoptera abundance | GLMMs | Negative binomial (log-link) | _ | Total forb cover (%) | 1\| Site |
| Margin | Lepidoptera richness | LMMs | Gaussian | _ | Total forb richness | 1\| Site |
| Margin | Bumblebee abundance | GLMMs | Negative binomial (log-link) | _ | Total forb cover (%) | 1\| Site |
| | | | | | % cover of Asteraceae | |
| Margin | Bumblebee richness | LMMs | Gaussian | _ | Total forb cover (%) | 1\| Site |
| Margin | Hoverfly abundance | LMMs | Gaussian | ln(x) | Total forb cover (%) | 1\| Site |
| Margin | Hoverfly richness | LMMs | Gaussian | _ | Total forb richness | 1\| Site |
| | | | | | % cover of other forbs | |

[1] Model abbreviations: GLMMs, generalised linear mixed-effect models; LMMs, linear mixed-effect models.

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